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Keeping up with Dobzhansky: G. Ledyard Stebbins, Jr., Plant Evolution, and the Evolutionary Synthesis

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ABSTRACT – This paper explores the complex relationship between the plant evolutionist G. Ledyard Stebbins and the animal evolutionist Theodosius Dobzhansky. The manner in which the plant evolution was brought into line, synthesized, or rendered consistent with the understanding of animal evolution (and especially insect evolution) is explored, especially as it culminated with the publication of Stebbins's 1950 book *Variation and Evolution in Plants*. The paper explores the multi-directional traffic of influence between Stebbins and Dobzhansky, but also their social and professional networks that linked plant evolutionists like Stebbins with Edgar Anderson, Carl Epling, and the 'Carnegie team' of Jens Clausen, David Keck, and William Hiesey with collaborators on the animal side like I. Michael Lerner, Sewall Wright and L.C. Dunn and other 'architects' of the synthesis like Ernst Mayr, Julian Huxley and George Gaylord Simpson. The compatibility in training, work styles, methodologies, goals, field sites, levels of analysis, and even choice of organismic systems is explored between Stebbins and Dobzhansky. Finally, the extent to which coevolution between plants and insects is reflected in the relationship is explored, as is the power dynamic in the relationship between two of the most visible figures associated with the evolutionary synthesis.

KEYWORDS - botany, plant evolution, animal evolution, evolutionary synthesis, organismic system, coevolution, scientific collaboration, field site, Mather, G. Ledyard Stebbins, Theodosius Dobzhansky

> *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. The task of the evolutionist, therefore, is to seek out and evaluate all these factors and processes in respect to as many different organisms as possible, and from the specific information thus acquired construct such generalizations and hypotheses as he can. This requires the broadest possible knowledge of biology, which, if it cannot be acquired through direct contact with original research, must be built up vicariously through communication with biologists in different fields.*
>
> G. Ledyard Stebbins, Jr.,
> 'Preface', *Variation and Evolution in Plants*, 1950.

The synthesis was the synthesis of genetics, systematics, paleontology, and Ledyard Stebbins.

Ernst Mayr

The last book of the evolutionary synthesis appeared in 1950.[1] In its synthetic aims and eventual influence it resembled the other books that brought in the evolutionary synthesis, but it also bore notable differences. It had none of the originality, inventiveness or the literary panache of G.G. Simpson's 1944 *Tempo and Mode in Evolution* that brought paleontology into the synthesis; it had none of the manifesto-like qualities or the spirited defense of the naturalist-systematist tradition of Ernst Mayr's 1942 *Systematics and the Origin of Species* that placed systematics on equal footing with genetics; nor did it have the expansive world-view building ambition of Julian Huxley's 1942 *Evolution: The Modern Synthesis.* It did, however, bear a striking resemblance to the first, and most important book that laid the groundwork for the evolutionary synthesis, Theodosius Dobzhansky's 1937 *Genetics and Origin of Species.* Written by a botanist, G. Ledyard Stebbins, Jr., the last book of the evolutionary synthesis titled *Variation and Evolution in Plants*, was the only taxon-defined book in the group that was explicitly designed to create a synthetic picture of plant evolution that emulated the synthesis of *Genetics and the Origin of Species*.[2]

The scope of the botanical project was vast. Botany (and the plant sciences) had seen an explosive growth at the turn of the century,[3] and the abundant insights gleaned from the plant world that had helped shape genetics, systematics, ecology, biogeography, and evolutionary theory in the first few decades of the twentieth century were also responsible for creating a disparate array of confusing data that thwarted a coherent and synthetic understanding of plant evolution.[4] Not only was the potentially relevant literature enormous, but plant evolution itself appeared subject to a range of special phenomena that made evolutionary processes especially complex. For one thing the variation patterns of plants seemed compli-

[1] For a complete list of books and for historical background on the evolutionary synthesis see Mayr and Provine 1980; Smocovitis 1996.

[2] For historical background on G. Ledyard Stebbins and the publication of his book see Smocovitis 1997; Smocovitis 1988. In numerous historical reflections, Stebbins explicitly stated that his book closely followed Dobzhansky and the wider evolutionary synthesis. Oral History Interview, Number VI; and see discussion below. See also Stebbins 1980.

[3] For the historical backdrop to botany and the plant sciences in the late nineteenth century see Rodgers 1944a; 1944b. The distinction between botany, plant science, and plant biology is made in Smocovitis 1992. For developments in the US see Smocovitis 2006.

[4] Popular accounts of plant evolution that included F.O. Bower's *Botany of the Living Plant* (1919) and W. Zimmermann's *Die Phylogenie der Pflanzen* (1930) drew heavily on morphology and paleobotany, but did not incorporate knowledge from genetics. They offered no account of the mechanisms for evolution.

cated; with open or indeterminate genetic systems, it was difficult to distinguish genotypic from phenotypic responses. As a result, a belief in Lamarckian or 'soft' inheritance had been widespread in botanical circles. In addition to this, many botanists were still confused about mutation theory, due in large part to incompletely understood genetics seen in complex organismic systems like *Oenothera*. Three additional phenomena posed special challenges to the formulation of a general theory of plant evolution: polyploidy (the multiplication of chromosome sets), apomixis (an asexual mode of reproduction common in plants), and hybridization. Although by no means exclusively found in the plant world, these phenomena occurred with regularity and interacted with each other to make for an especially complex pattern of evolution that bedeviled botanists and plant scientists in the early decades of this century.[5]

Stebbins's formulation of plant evolution in *Variation and Evolution in Plants* recognized the especially difficult nature of the synthetic project and the ever-growing literature. For this reason, Stebbins initially described the book for his readers as a 'progress report'. To formulate his synthesis, Stebbins had drawn heavily on the framework set forth by Dobzhansky in *Genetics and the Origin of Species*. The most notable instance of Dobzhansky's influence in *Variation and Evolution in Plants* is the strong presence of what was eventually termed Dobzhansky's 'biological species concept'.[6] Where classical or herbarium taxonomists had mostly adhered to the morphological species definition, and other more ecologically-minded botanical 'biosystematists' had attempted more complex schemes based on different configurations of reproductive isolation, Stebbins was one of the first botanists to explore the potential application of Dobzhansky's dynamic species definition in plant evolution.[7] This application was no easy matter, given the fact that elaborate mating systems displaying polyploidy, apomixis and hybridization, which served to blur discontinuities, made determination of species especially difficult in the plant world. In accordance with Dobzhansky's general framework of evolution, Stebbins argued that the variation and

[5] For one attempt to formulate a general theory of evolution that drew heavily from plants see Lotsy 1916.

[6] The 'BSC' was elaborated by E. Mayr in his 1942 contribution to the evolutionary synthesis (Mayr 1942).

[7] Major reproductive-isolation configurations included concepts like the ecotype, ecospecies, and the comparium. The leading proponents of such reproductive-isolation based configurations in the 1930s and 1940s included the team of Jens Clausen, David Keck and William Hiesey and biosystematists Wendell Camp, and Charles L. Gilly. Other adherents of Dobzhansky's biologically-based species definition, included Verne Grant, and Friedrich Ehrendorfer. See Grant 1957 for a clear discussion of the merits of the biological species concept versus the morphological concept.

evolution of plants was the outcome of natural selection operating at the level of small individual differences across the continuum of microevolution and macroevolution. Stebbins's analysis thus purged botany of its adherence to Lamarckism and other confusing theories like mutation theory in favor of the primary mechanism of natural selection. Rendering plant evolution compatible with evolutionary examples from birds, mammals or insects was the major accomplishment of *Variation and Evolution in Plants,* in addition to extending and fortifying Dobzhansky's general theory with plant examples, and practically inventing the new field of plant evolutionary biology.[8] The 'progress report' was in fact not only the last book of the evolutionary synthesis, but it was also longest: it was 643 pages in length and included over 1,250 citations.

In formulating his analytical framework, Stebbins had drawn heavily from individuals like C.D. Darlington (1903-1981) and his conception of evolving genetic systems to reconceptualize the phenomena of polyploidy, apomixis and hybridization (Darlington 1939). He had also drawn on the work of biosystematists interested in a more dynamic ecological understanding of plants in nature, and his close friend the systematic botanist Edgar Anderson (1897-1967) whose views of plant evolution closely resembled his own.[9] But his main source of inspiration was Dobzhansky and his 1937 book. Dobzhansky had drawn upon some notable plant examples and made an attempt to include discussion of plant evolutionary mechanisms, but his book was by no means heavily concerned with phenomena like polyploidy, apomixis and hybridization – and their special interactions in many plant species – to an extent that would shed light on the complexities of plant evolution. For the most part, it was primarily concerned with establishing orthodox mechanisms and patterns of evolution prevailing in much of the animal kingdom. Thus, although there was discussion of phenomena like asexual reproduction, hybridization, polyploidy or general processes and mechanisms of evolution that 'violated' species barriers and gave rise to reticulating or anastomosing processes (all of which formed part of the common pattern of plant evolution), it tended to view these phenomena as special cases of evolution 'unique' to plant evolution, especially present in 'higher' plants. For Dobzhansky, the dominant pattern of evolution was that commonly seen in animals. In particular, *Drosophila,* Dobzhansky's preferred and closely studied organism, increasingly set

[8] A historical assessment of *Variation and Evolution in Plants* is found in Raven 1974 and Solbrig, Jain, Johnson and Raven 1979. See also Smocovitis 1988.

[9] For a discussion of Edgar Anderson's involvement in the evolutionary synthesis see Kleinman 1999.

the standard for a typical evolutionary system. How and why did Stebbins choose to follow Dobzhansky's 'lead', given the doubly difficult task of creating a coherent theory of plant evolution, and one which was also compatible with animal evolution at that? How and when exactly did Dobzhansky and Stebbins reconcile the different views of evolution in plants and animals? What was the nature of the relationship between the two? And in what manner did their personal relationship influence their science? In a draft manuscript of his autobiographical reflections, Stebbins explicitly noted the extent of Dobzhansky's influence on him:

> Nobody can deny that the leader of the mid-century storm of interest in evolutionary theory during the middle of the 20th century was Theodosius Dobzhansky. He was the only scientific evolutionist who combined a thorough knowledge of what was then modern genetics based on the research and theory exemplified by the research of T.H. Morgan and his associates, with a [sic] extensive knowledge of a deep interest in the forces of evolution that operate in nature. Dobzhansky was enormously persuasive; like all examples of Messianic promotion of a cause, his enthusiasm was captured captivating? infectious? [sic] Furthermore, he had planned a campaign that would supplement his own writing with that of specialists in related fields like G.G. Simpson, Ernst Mayr and myself to produce a well balanced synthesis of contemporary theories.[10]

Dobzhansky's ability to attract or draw followers to his views and his 'charismatic influence' has been noted by historians of science (Levine 1995). Was this 'Messianic promotion' the sole reason Stebbins chose to follow Dobzhansky's lead? Or were there a range of other factors including important points of scientific agreement at play? Was the relationship as one-sided as the above quotation suggests, or was there a more complex multi-directional traffic of influence that involved other individuals?

Ideally, one place to look for answers is in correspondence between Dobzhansky and Stebbins during this critical interval of time, but what little may have existed has been lost.[11] Certainly nothing resembling the superb historical record of interaction left in Dobzhansky's correspondence with Sewall Wright, examined in detail by William B. Provine in his biographical study of Sewall Wright has been found (Provine 1986).

[10] G. Ledyard Stebbins, 'The Lady Slipper and I', unpublished draft manuscript. Quotation on p. 119. The typescript includes the word 'captured'. This is crossed out and the words captivating? infectious? are handwritten on the top. Manuscript dated approximately 1998, in author's possession.

[11] According to Stebbins a house fire destroyed much of his early correspondence; there is no significant correspondence until the 1960s between Stebbins and Dobzhansky in the Dobzhansky papers at the American Philosophical Society Library.

Other sources can be similarly employed, however, to help us understand at closer range how and when Dobzhansky and Stebbins interacted and how their views came to resemble each other. In this paper, I attempt to trace out the historical circumstances of the Dobzhansky-Stebbins interaction using a variety of available sources. Because Stebbins chose to follow Dobzhansky's 'lead', and because Dobzhansky's life has been mapped out extensively by historians,[12] I will focus on the Stebbins side of the interaction. As will become apparent, Dobzhansky did in fact exert a strong, and in fact a critical influence on Stebbins. Their relationship was not, however, a simple 'one-sided' affair. Instead, it involved a complex, multi-directional traffic of influence that depended on agreement over specific scientific points, shared commitments to a unified general theory of evolution, similarities in work styles and habits, compatible personalities, and an active network of friends and acquaintances seeking knowledge of both plant and animal evolution.

Dobzhansky and Stebbins: First Encounters, 1936-1939

Stebbins recalls being not terribly interested in Dobzhansky's early work on *Drosophila melanogaster*. Any sort of special attraction was definitely missing at their first meeting during the spring of 1936 when Stebbins was invited by Thomas Hunt Morgan (1866-1945) to give a seminar at the California Institute of Technology. At the time, Dobzhansky was actively involved in working on crossover frequencies in mutants of *Drosophila melanogaster.* Stebbins recalled that Morgan had praised his 'Russian discovery', going so far as to describe him as a 'true genius'.[13] Both Dobzhansky and his wife Natasha were in the laboratory examining chromosomes when Stebbins was introduced to them. The meeting did not go beyond an introductory conversation because Stebbins saw little in Dobzhansky's work that interested him. He had not been following Dobzhansky's work closely and was not aware, or had not yet realized, that Dobzhansky was just beginning the

[12] There is no full scale biography of Theodosius Dobzhansky, but there is a stunning assortment of historical literature available on aspects of his life and work. This literature includes: Adams 1994; Ayala 1976; 1985; 1990; Ayala and Prout 1977; Ehrman 1977; Land 1973; Levene 1970; Levine 1995; Lewontin, Moore, Provine and Wallace 1981.

[13] Stebbins (1995) recounts this first meeting; see the account in the Oral History Interview, Number III, 1987; and see the recollection in his recent draft manuscript of his autobiography, 'The Lady Slipper and I.' Manuscript dated approximately 1998, in author's possession.

work on what would be later known as 'Genetics of Natural Populations', or the 'GNP' publication series. This was the ambitious study to understand the genetics of evolutionary process in natural populations of *Drosophila*; ironically, this was the work that brought them closer together in the next decade.[14]

At the time of the meeting, Stebbins was 'junior geneticist' to E B. Babcock (1877-1954), the plant geneticist, and founder of the genetics department at the University of California Berkeley.[15] During 1917-1918, Babcock had begun his critically important work on the genetics of the genus *Crepis*, a member of the chicory tribe of the Compositae. Lasting until the late 1940s, the project was initially launched with the goals of securing an organismic system from the plant world that would attain the success of *Drosophila melanogaster.*[16] With the aid of a series of coworkers, the most well known of which was Michael Navashin (1857-1930), who brought mutant stocks of *Crepis* from Russia with him, the project grew to encompass the methods of systematics, genetics, and ecology in the 1920s. By the 1930s, the *Crepis* project had grown into a massive interdisciplinary undertaking not just to work out the phylogeny of the complex genus, but also to understand the genetic basis of evolutionary change. With the support of a Rockefeller Foundation grant, Babcock secured the appointment of Ledyard Stebbins, a recent graduate of Harvard botany, and a teacher of biology at Colgate University to help with the cytological and systematic work on the genus. Although his background was in floristics and botanical systematics, Stebbins had been turned on to cytogenetics by geneticist Karl Sax (1892-1973) while still a student at Harvard, and had begun studying the cytogenetics and systematics of the peony genus, *Paeonia*, shortly after graduating from Harvard. In July of 1935, Stebbins joined the *Crepis* project, with considerable experience in cytogenetics, and quickly made significant contributions to Babcock's project. In addition to increasing the emphasis on study of geographic distribution of the

[14] For historical discussion on the significance of the 'GNP' series see Lewontin *et al*. 1981.

[15] The 'Prospectus of the College of Agriculture' for 1936-37 described Stebbins as 'Junior Geneticist to the Experiment Station'.

[16] See E.B. Babcock to G.H. Shull, letter dated September 23, 1915. University of California, Genetics Department. Folder titled Babcock to G.H. Shull 1911-1943. Genetics Department Papers. Babcock's rationale is explained in a 1920 paper. See Babcock (1920). Although it was enormously productive in the way of generating monographic material, *Crepis* never attained the status of *Drosophila* as model organism. In part this was because the generation times were too long, the plant required extensive space, and also because the genetic system was too complex to serve as the standard model for evolution. Babcock's crowning achievement was *The Genus Crepis*. Part One and Two. University of California Publications in Botany, volumes 21 and 22, 1947.

genus, and sorting through some New World relatives of the genus, Stebbins articulated the notion of the 'agamic complex', a special case of what became his 'polyploid complex', a concept explaining the formation and geographic distribution of diploid and polyploid forms of plant species like *Crepis*.[17]

Although neither explicitly noticed it at the time, both Dobzhansky and Stebbins actually occupied fairly similar niches in their professional and scientific lives at the time of their meeting. Neither had early formal training in genetics, but both were drawn to genetics eventually, and became junior assistants on projects with senior figures who were the pioneers of American genetics in their generation. Both Dobzhansky and Stebbins were in fact asking similar questions of the evolutionary process and seeking to integrate methods from genetics, cytology, and systematics, with consideration of the natural populations of their organisms. Both were also at critical transitional stages in their professional and intellectual lives and were about to emerge as leaders in their own right. Being somewhat further ahead than Stebbins, Dobzhansky had already received a range of offers that spring, each of which he declined to stay at the California Institute of Technology. This showed that he was already a force of his own, a fact borne out by his receiving an invitation to give the prestigious Columbia-based Jesup Lectures that spring (delivering them only six months later to be published as *Genetics and the Origin of Species* the following year). Most importantly, Dobzhansky completed two of the first papers which laid the foundations for the launching of the GNP series that spring and sent them out shortly after the meeting with Stebbins.[18] The new project promised by these two papers describing the chromosomal inversions on chromosome three of geographic races of *D. pseudoobscura* and the suggestion that these could be used to reconstruct phylogenies, in fact bore a startling resemblance to the *Crepis* project. At a fundamental level, therefore, Dobzhansky and Stebbins shared the same goal to understand the genetical basis for the origin of biological diversity within their respective organisms.

Dobzhansky and Stebbins, furthermore, had similar background preparation. Although they studied the evolutionary process through cytogenetic methodology, both were keen naturalists with a deep knowl-

[17] More specifically, the term referred to a complex of reproductive forms centering on sexual diploids surrounded by apomictic polyploids. See Babcock and Stebbins Jr. 1938.

[18] According to Provine, the first paper studying the geographical distribution of inversions on the third chromosome of *Drosophila* was sent out June 8, 1936. For a fuller history of the GNP series see Provine 1981; and see pages 5-83 in Provine, 1986.

edge of systematics and a sensitivity to geographic variation patterns. Like Dobzhansky, who had formal early training in systematics, Stebbins began his career training in systematic botany, phytogeography, and even morphology, before he began his work in evolutionary cytogenetics. Though they had taxon-based identities - Dobzhansky as zoologist and Stebbins as botanist – both moved freely between organismic systems as their choice of problems dictated. Thus, Dobzhansky began his systematic studies on the Coccinelidae, the lady-bird beetle family, moved to *Drosophila melanogaster*, *Drosophila pseudoobscura*, and other species of *Drosophila,* but also on occasion worked with plants like *Linanthus parryae* and *Arctostaphylos* sp., if they served his purposes. Stebbins also made similar shifts in study organisms; though he became associated with the systematics, genetics, and evolution of the complex Aster family, the Compositae, he also worked with grasses and peonies. Thus, though they were both organism-oriented biologists, they never made a full-scale commitment to any one organismic system exclusively. What some biologists may describe as a form of 'taxonomic promiscuity' or 'organismic opportunism', in fact had a strongly defined rationale: both men had made their first and strongest commitments to understanding evolutionary mechanisms at the most ultimate level available to them at the time. Operating at the ultimate, and deepest level of the evolutionary process, in turn made it possible to make generalizable insights that could feed into a unified theory of evolution. The principles of genetics, were universal, no matter what the organismic system employed.[19] This was a critical attribute both shared even early on in their careers, unlike other biologists who remained loyal to working with one organismic system exclusively.

Though they were comfortable with laboratory work, both additionally lacked the kind of manual dexterity and love of precision that were hallmarks of great laboratory-oriented experimentalists; Dobzhansky's 'sloppiness' in laboratory preparations was noted by his co-workers, and Stebbins early on recognized that he was awkward with his hands.[20]

[19] Dobzhansky introduced his portion of the 1944 Carnegie monograph on *Drosophila pseudobscura* he wrote with Carl Epling with the following: 'The mechanisms which control heredity are fundamentally the same in all organisms, no matter to what subdivision of the animal or of the plant kingdom they belong; the principles of genetics are perhaps the most universal of all biological principles' (Dobzhansky, Epling 1944, 3).

[20] See in particular the letter about Dobzhansky's technique by E.W. Novitski to Provine dated December 1, 1979, discussed in Provine (1981). Stebbins admitted that he had a hard time with doing things that required delicate manipulation with his hands in his oral history interviews. Oral History Interview, Number II, 1987.

Both also lacked quantitative orientation; Stebbins's reaction to first seeing Sewall Wright's diagrams representing what became his shifting balance theory of evolution at the 1932 International Congress of Genetics was not unlike Dobzhansky's: he recognized their importance, but had no clear idea of what they meant.[21] Both also shared an impatience, distaste and even occasional hostility to the classical methods of taxonomists which they viewed as static, artificial attempts to create utilitarian, and artificial classification schemes. Their own experiences as naturalists (Dobzhansky from his Russian days, and Stebbins from his early experiences in New England) had led them both to seek a dynamic, population-oriented, understanding of natural populations in order to construct evolutionary phylogenies. Even their collecting sites began to converge as both focused on western distributions, altitudinal, climatic and edaphic variations in their respective organisms.

As social creatures too, they also had much in common: both were keen networkers and communicators who traveled in wide biological circles. Rarely satisfied with insights gleaned from their own narrower research programs, both sought the company, assistance, and expertise of other workers to widen their understanding of general evolution. Both were voracious readers who were conversant with a diverse body of literature drawing on many organismic systems, levels of analysis, and different methods in the biological sciences. In short, when the two met, they already had a great deal in common although they may not have been aware of it at the time. On the surface, at least, the primary difference at the time of meeting was that Dobzhansky was working on the genetics of a well-known insect model organism (*Drosophila)* while Stebbins was using cytogenetics to reconstruct the phylogeny of a complex plant model organism that was to serve as the plant equivalent of *Drosophila,* namely *Crepis*. Given the number of similarities, and the fact that the number of young and energetic evolutionists and geneticists in California was actually quite small, it was probably only a question of time before Stebbins and Dobzhansky were drawn more closely together. Both had common goals to understand evolution at the ultimate genetic level of evolutionary change in their respective organismic systems in order to formulate a general theory of evolution.

Several factors set the stage for converging interests between the two following their initial meeting: the publication of Dobzhansky's 1937 book bringing a synthetic view to evolution, Dobzhansky's growing interest in plant evolution through his friendship and collaboration with

[21] Oral History Interview, Number III, 1987.

the UCLA botanist Carl Epling (1894-1968), the opportunity for Stebbins to teach a course in general evolution, and a mutual friendship with the Russian émigré geneticist, I. Michael Lerner (1910-1977).[22] In the late 1930s, Dobzhansky frequented the San Francisco Bay area to visit his close friend Lerner, who had completed his Ph.D. in 1936 in poultry genetics at Berkeley and subsequently stayed there. Both were Russian-speaking refugees who had found themselves in Vancouver, British Columbia, Canada in 1931. Dobzhansky was stranded there while waiting for an entry visa to the US, and Lerner was receiving undergraduate training while waiting for entry into the US. Sharing their immigration hardship (Lerner's job as a student there was to dig ditches and tend the chickens on the farm at the University of British Columbia),[23] they became close friends and sought each other's company for years after. Finally receiving an invitation to study at Berkeley in 1933, Lerner, along with another graduate student Everett R. Dempster (Babcock's teaching assistant at the time) organized a monthly journal club they called Genetics Associated.[24] It included mostly graduate students and other younger researchers interested in genetics on the Berkeley campus. Stebbins recalled joining the group in 1935 just after he arrived in Berkeley.[25] The group was led mostly by Lerner, and meetings were held every month, with two or three recent papers chosen for discussion. The group included research associates from the *Crepis* project, like James Jenkins, Donald Cameron, a research assistant to Roy Clausen, then studying the genetics of *Nicotiana tabacum*, along with plant breeders Francis Smith and Alfred Clark. It was through Genetics Associated that Stebbins became close to Michael Lerner and in turn it was through Lerner that Stebbins became reacquainted with Dobzhansky who frequently visited the Bay area to lunch with Lerner. Although Dobzhansky and Lerner spoke in Russian, with only occasional conversations in English, Stebbins could pick out enough of their conversation to understand their interests. Through these meetings, Stebbins began to understand Dobzhansky's recent interest in, and collaboration with, Sewall Wright and the GNP.

Stebbins had also become acquainted with Dobzhansky's new syn-

[22] Lerner was born in Harbin, Manchuria of Russian parents. Manchuria was under Chinese control at the time. For a recent biographical profile of Lerner see Smocovitis, in press.

[23] Lerner's reminiscence is reproduced in his National Academy of Science biographical essay: Allard 1966, 166-175.

[24] Oral History Interview, Number IVa, 1987.

[25] He continued to participate in the group until it disbanded in the early 1950s, its members having dispersed around that time.

thesis of genetics and evolution by reading *Genetics and the Origin of Species* around the time of its first appearance in 1937. Among the exciting insights he gleaned from the volume was a dynamic view of evolution that it made possible. Especially exciting was the reconceptualization of species as stages in biological evolution which formed as the product of the formation of sterility barriers. Such a conceptualization opened the doors for understanding mechanisms of speciation. This insight came at a critical time for Stebbins as he tried to understand speciation patterns in *Crepis.* The new, more biological - and therefore deeply genetical definition – permitted a deeper understanding of the mechanisms leading to speciation. The alternative, the morphological conception of species, gave little hope for understanding the genetical basis of species formation and reeked of the older static herbarium taxonomy. The new biological and dynamic view of species that Dobzhansky introduced thus had potential to illuminate the mechanisms and process of speciation and was a critical concept that Stebbins found productive. Within a year, Stebbins wholeheartedly applied Dobzhansky's insights into species formation in the monograph of *Crepis* that he wrote with E.B. Babcock; instead of stressing the differences between *Crepis* species-formation (it was an apomict which frequently hybridized and formed polyploids) and conventional animal evolution, he chose to focus on the similarities. Stebbins and Babcock's explanation of the novel 'agamic complex' (a complex of reproductive forms centering on sexual diploids surrounded by apomictic polyploids) was stated in the following quotation: 'The species, in the case of a sexual group, is an actuality as well as a human concept; in an agamic complex it ceases to be an actuality.' They closed with an evocation of their source of inspiration: 'The same conclusion about apomictic groups has been reached by Dobzhansky' (Babcock and Stebbins Jr. 1938).

Although he eagerly read Dobzhansky's book and was greatly impressed by the general theory and synthetic cast of the volume as a whole, Stebbins recalled that he found little in the way of understanding for plant evolution directly. At best, the book promised the possibility of a general theory of plant evolution. Stebbins felt the need to integrate plant evolution with knowledge from animal evolution increasingly from 1939 on, when he was offered a teaching slot for Genetics 103, 'Organic Evolution', taught out of the Genetics department at Berkeley. With Babcock's advocacy, and because the Rockefeller grant ran out after four years, Stebbins was offered the teaching slot and a position as assistant professor at Berkeley in 1939. Teaching the general course in evolution out of the genetics department was the perfect opportunity to read widely. Under the pressure to put together a reading list that also explained plant evolution,[26] Stebbins, a voracious reader, consumed existing literature in evolution, especially seeking literature that would be suitable for an evolution course, taught out of the College of Agriculture. The reading list for his course in spring 1940, only recently located, indicated that he assigned Dobzhansky's *Genetics and the Origin of Species* for Part IV of his course ('The Dynamic Phase of Evolution'). He also assigned extensive other material for his students including the first edition of Darwin's *Origin*, A.F. Shull's 1936 *Evolution*, J.B.S. Haldane's 1932 *The Causes of Evolution*, T.H. Morgan's 1935 *The Scientific Basis for Evolution* (the second edition), and H. De Vries's 1910 *The Mutation Theory*.[27] Additional botanical references were included in other parts of the course.[28]

As Stebbins explored the general literature on evolution, Dobzhansky was keeping up with the growing literature in plant evolution. This was the result of an increasing interaction with UCLA-based systematic botanist Carl Epling. Approximately in 1939-1940, Dobzhansky had approached Epling for help in understanding the geographic distributions of inversion frequencies in the third chromosome of the species then known as *Drosophila obscura*.[29] Epling was a logical choice: not only was he close by at UCLA, but his own interests were starting to take a more evolutionary direction in the 1930s.[30] Like Stebbins and Dobzhansky he was among a group of systematists beginning to embrace the 'new' systematics, which stressed evolutionary and genetical approaches to constructing phylogenies. Epling also had a deep knowledge of the local flora and was especially adept at interpreting distribution patterns.[31] Epling and Dobzhansky thus began to collaborate on *Drosophila* as well as a study on the microgeographic races of the plant *Linanthus parryae* in the early 1940s as part of the GNP work. The conversations with Epling, who followed the growing

[26] The Zoology department offered its own evolution class.

[27] Document titled 'Genetics 103, Spring Semester, 1940. Tentative Outline of Course.' Box, 13. Stebbins Jr. Papers.

[28] Botanical references included: Bower 1930 and Zimmermann 1930.

[29] Epling's first meeting with Dobzhansky is described in his interviews with Anne Roe. Anne Roe Papers. Folder titled Carl Epling.

[30] Epling had been one of the original participants along with R. A. Emerson, Dobzhansky and Julian Huxley, at the symposium titled ' Speciation' in 1939 at the AAAS meetings in Columbus, Ohio. This was the meeting that would see efforts to organize systematists into the Society for the Study of Speciation. See Smocovitis 1994.

[31] Rudi Mattoni, personal communication. Mattoni had been a graduate student of Epling's in the early 1950s.

literature on plant evolution by younger workers like Stebbins, led to Dobzhansky's growing appreciation of plant evolution. Thanks largely to Epling, the 1941 revised edition of *Genetics and the Origin of Species* included an impressive amount of recent data on plant evolution. In fact, the closing sentence of the book, which discussed the prevalence of the biological species concept as it applied to the plant world, known to include a number of problematic asexually reproducing forms like 'agamic complexes', relied on the recent monograph on *Crepis* from Babcock and Stebbins. Dobzhansky quoted: 'As pointed out by Babcock and Stebbins (1938), "The species, in the case of a sexual group, is an actuality as well as a human concept; in an agamic complex it ceases to be an actuality."' Thus, the insights from Dobzhansky that had fueled Stebbins and Babcock's analysis of *Crepis*, came back as proof of Dobzhansky's general theory. From Dobzhansky's perspective, therefore, the literature of plant evolution which he was learning from Epling, could in fact be used to buttress and support his general theory, especially given the complex evolutionary mechanisms prevalent in plants. In fact, in 1941, it provided some of the strongest support for his views.

In turn, Stebbins's voracious reading of the evolution literature, combined with the conversations he heard between Lerner and Dobzhansky (now more cognizant of plant evolution) was instrumental to Stebbins's turn of interests. In addition to learning more about the work of mathematical theorists like Sewall Wright through Dobzhansky, he also learned of the work of R.A. Fisher (1890-1962), and J.B.S. Haldane (1892-1964). It was also at this time that he learned of the contributions of Sergei Chetverikov (1880-1959) and others associated with the Russian school of population genetics that had been crushed by the Stalinist regime. By the early 1940s, Stebbins became more and more informed of the exciting developments in evolution both through his contact with Lerner and Dobzhansky, and through increasing interactions with other interested scientists in the Bay area. Though they weren't expressly aware of it initially, all had been part of the wider movement to reform the systematic study of life that Julian Huxley called the 'new' systematics (Huxley 1940).

The 'Dynamic Phase of Evolution': 1939-1946

The San Francisco Bay area as a whole became a bustling center of evolutionary activity from the late 1930s on. A loosely-based organization which came to be known as the 'Biosystematists', began approximately in 1937. It drew together interdisciplinary workers from varied departments at Berkeley, Stanford University, the Stanford-based Carnegie Institution and other institutions in the Bay area.[32] The group met once a month at rotating institutions and drew on information from diverse animal systems as well as plants. Botany and plant evolution was well represented among the members, especially due to the strong presence of the Carnegie 'team' of Jens Clausen (1891-1969), David Keck (1903-1995) and William Hiesey (1903-1998), who were engaged in an interdisciplinary project of their own to understand plant evolution. By the early 1940s the Biosystematists had become the clearing-house for evolutionary interests for the west coast of the US, the members becoming instrumental in leading the west coast contingent of national, and in fact, international efforts to organize evolutionists and to create an international society with a scientific journal.[33] The group also included frequent visitors to the Bay area like the botanical systematist Carl Epling from UCLA, and the botanical systematist Edgar Anderson from the Missouri Botanical Garden, one of Stebbins's closest and most influential friends.

Dobzhansky's visits to Lerner and the Bay area were temporarily interrupted in 1940, however, when Dobzhansky left the California Institute of Technology to become professor of Zoology at Columbia University. The outbreak of the war shortly after also temporarily thwarted movements and activities across the country, but with the aid of Carnegie Institution grants, Dobzhansky continued to visit collecting sites in the western US, especially California. According to Stebbins it was in the summer of 1944 that he began his 'close, intimate, and highly profitable association with Dobzhansky' (Stebbins 1995), which intensified over the next couple of years. By that time, Dobzhansky was well into his GNP series and collaborating with Sewall Wright. Critically important for the GNP series, Wright and Dobzhansky increasingly were moving away from an interpretation of their results on the distributions of inversions in terms of strictly genetic drift and towards interpretations based on geographic and ecological determinants. Dobzhansky was also exploring variations in desert and mountainous populations of *D. pseudoobscura* in regions of California that were familiar to Stebbins and other west coast botanists like Epling studying the

[32] The history of the Biosystematists is recounted on pages 95-97, in Lincoln Constance, 'Versatile Berkeley Botanist. Plant Taxonomy and University Governance.' An Oral History Conducted in 1986 by Ann Lage, Regional History Office, The Bancroft Library, University of California, Berkeley, 1987. I discuss the Biosystematists at greater length and include membership and a photograph in Smocovitis 1997; see also Hagen 1984; Lidicker Jr. 2000.

[33] For a detailed history of these efforts to organize evolution see Smocovitis 1994; Cain 1993.

variation patterns in the California flora. In one recollection, Stebbins – an ardent selectionist from Harvard days – explicitly recalled his shift of interest to Dobzhansky's work at this time:

> Of special interest was the inversion content of populations from the desert margin in southern California: Andreas Canyon near Palm Springs, Piñon Flats at 900 meters near the foothills for San Jacinto Mountains, and Idylwild, at 1800 meters in these mountains themselves. I clearly saw with him [Dobzhansky] that here was an unusual opportunity to study Darwinian natural selection in a species in which hypothesis could be tested under controlled conditions. (Stebbins 1995, 9)

During the summer of 1944, Dobzhansky was collecting *Drosophila pseudoobscura* and *Drosophila persimilis* along the experimental transplant sites originally established in the 1920s and 1930s by Harvey Monroe Hall (1874-1932), and taken over by Jens Clausen for the experimental study of plant evolution in *Achillea* and *Potentilla.*[34] Under the auspices of the Carnegie Institution, the three sites for the altitudinal studies of variation were: Stanford (at 30 feet), Mather (at 4,500 feet), and Timberline (at 10,000 feet). In the midst of a beautiful forest, with cabins (one of which had a laboratory), Mather was the base camp for all operations. In the early 1940s, Dobzhansky took advantage of the Carnegie Institution's installation for his research and arranged to stay there off and on for subsequent summers. (Fig. 1)

Fig. 1 – Theodosius Dobzhansky at Mather, approximately 1965. Courtesy G. Ledyard Stebbins Jr.

[34] See Smocovitis 1988 for more historical discussion on Hall and Clausen. See also Hagen 1984.

By 1944 Stebbins had long finished his work on *Crepis*, and, partially as a response to pressures stemming from the war, was well into his major project to breed better forage grasses. This involved detailed studies of natural hybridization in native grass species like *Elymus glaucus*, or wild rye grass and *Sitanion hystrix*, squirreltail, which he was also producing in experimental plots. Stebbins was also continuing to read voraciously in preparation for his evolution course at Berkeley, which he continued to teach through the 1940s, even as enrollments were decreased during the war years. (Fig. 2) When he found out that Dobzhansky had made arrangements to spend the summer at Mather, Stebbins recalls taking the opportunity for research and study with Dobzhansky and he 'looked forward eagerly to sitting at the feet of the great evolutionist, and absorbing knowledge from him' (Stebbins 1995, 10).

Fig. 2 - Theodosius Dobzhansky on horseback at Mather, 1951. Courtesy G. Ledyard Stebbins Jr.

In his oral history interviews, Stebbins gave an especially vivid picture of this first summer with Dobzhansky (Fig. 3).

Fig. 3 - Theodosius Dobzhansky collecting *Drosophila* with E.B. Ford, at Mather, 1951. Courtesy G. Ledyard Stebbins Jr.

I heard that he [Dobzhansky] was in Mather, and decided as a teacher of evolution, I needed to sit with the great man and get some pearls of wisdom. I sent him a note, telephoned and I asked him if I could do so, and he said: 'Yes.' And I drove up and very quickly found that one did not sit at the feet of Dobzhansky. Because his day existed of sleeping, getting up, having a quick breakfast, checking the cups in which he had left out the bait for the *Drosophila*, collecting the flies, then making preparations from the flies from the previous collection, looking at the preparations for their positions of their inversions, to identify the inversions. That occupied the whole morning. In the afternoon, after lunch before the fly collecting, he went down to the stables and got on a horse and rode rapidly in some direction. The only way you could commune with him was by getting on another horse and riding equally rapidly in the same direction. Fortunately I had been riding horses when I was at school as a boy, the Cate school, so I could do that. And on that very first day, we rode up to a meadow about five or six miles away, where there were grasses belonging to the group that interested me in particular, the wheat grass group, woodland wild rye, and squirreltail. And when I saw this mass of beautifully flowering grasses of that group, I suspected there would be hybrids between those two species which almost always are when they come together, and they are sterile hybrids. So I rode my horse into the patch of grass, and while the horse was quietly munching on the object of my interest, I leaned down from the saddle and picked a woodland wild rye, urged the horse onto another little place, and there picked a cull of the squirreltail. Then I saw an intermediate-looking one from the saddle. I picked that also, and sitting in the saddle, I took them apart and looked at the glumes and discovered I really did have the hybrid. So I rode up to him and explained my story. I glowed, he said: 'Stebbins, you have made a great discovery. You are the first person who has seen, collected, and identified a hybrid from the back of the horse.' From then on I was up. You know, Dobzhansky's friends were strongly dichotomized. They were either white or black, and I was always on the white side, and it started with that actually.[35]

Yet another story from that summer recounted by Stebbins, reveals much about the way that Dobzhansky and Stebbins negotiated potential points of conflict. In this case they discussed the relative importance of hybridization in evolution in a friendly, playful manner that defused tension over differences they had in animal and plant evolution. According to Stebbins, Dobzhansky was playfully critical of the wastefulness of plants in producing so many sterile hybrids: '*Drosophila* orders things much better', he quipped to Stebbins. Stebbins 'retorted' with an explanation for plant hybrid sterility, and with a challenge to count the number of seeds actually produced on the sterile hybrids. According to Stebbins, Dobzhansky and his daughter Sophie (later Sophie Dobzhansky Coe) zealously thrashed and beat seeds for an hour to recover '28 seeds, out of a possible 10,000 to 15,000' (Stebbins 1995, 11).

Through the summer of 1945, Stebbins continued to follow Dobzhansky and his work closely, and visits to Mather continued into the 1950s, 1960s, and even into the 1970s, sometimes including small conferences that came to be known as 'Mather' symposia that included visitors like E.B. Ford, Hampton Carson, and others. (Fig. 4) In her published reminiscence of her father, Sophie Dobzhansky Coe recalled the summers she spent as a child at Mather, her father's intense work-habits, and his love of horseback riding. (Fig. 5) She explicitly recalled Stebbins's frequent visits:

Ledyard Stebbins was a frequent visitor to Mather and used to go on horseback rides with us. I remember some passionate discussions about the hybrid and introgressive status of the manzanita bushes our horses were passing, starting with the gray-leaved *Arctostaphylos manzanita* near the cabin and gradually changing to the shiny green foliage of *Arctostaphylos patula* as the trail climbed past the gigantic sugar pine into the canyon that led to the park gate. (Dobzhansky Coe 1994, 27)

The passionate discussions about the manzanita hybrids were fueled also by Epling's life-long interest in the group. In 1953 these discussions led to Dobzhansky's sole single-authored botanical paper. It is especially revealing of his view of plant evolution (Dobzhansky 1953, 73-79). The paper examined the distribution of the hybrids and parental forms between the same two species of *Arctostaphylos* along defined altitudi-

[35] Oral History Interview, Number III, 1987.

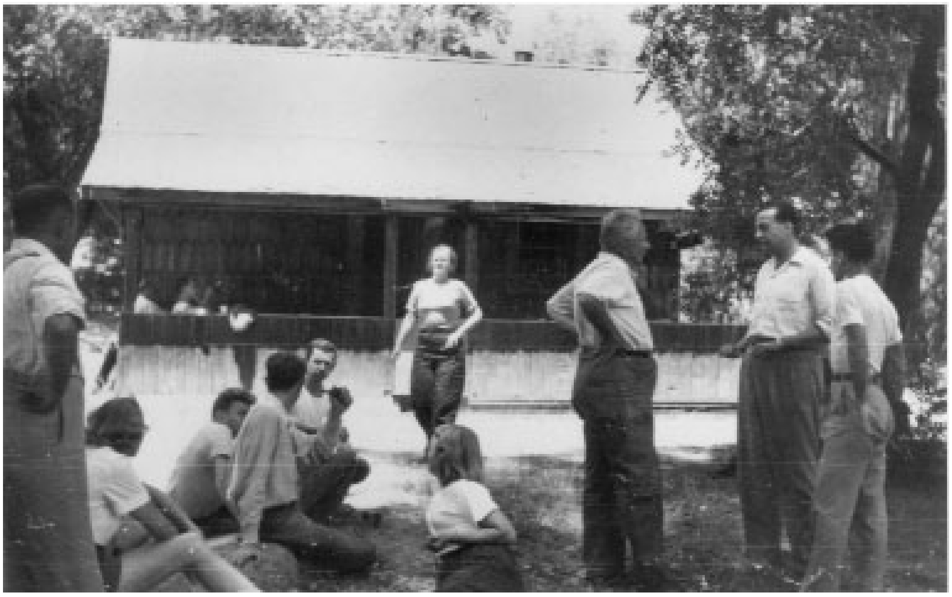

Fig. 4 - Group photo at Mather, 1950. Courtesy Paul Levine.

Fig. 5 - Theodosius and Sophie Dobzhansky on horseback, at Mather, 1951. Courtesy G. Ledyard Stebbins Jr.

nal transects. Using mostly morphological characters, he found that although the hybrids were not sterile, they were mostly F_1, rather than F_2 backcross products, and constituted no more than 10% of the populations in regions where both parents occurred. Not surprisingly, Dobzhansky used these data from *Arctostaphylos* to argue that the parents were coherent genetic systems which were capable of producing fit hybrid F_1s but experienced breakdowns in the F_2s. This not only supported his own 'biological' view of species, but also argued *against* Edgar Anderson's contentious theory of introgressive hybridization, a theory supported by few zoologists.[36] Dobzhansky's only botanical paper was thus mostly an opportunistic assault on introgression, a phenomenon commonly observed in plants which violated strict species boundaries. Dobzhansky's own view of evolution thus remained dominated by insect examples drawn from *Drosophila* and the theoretical models of his collaborator, Wright.

Even Dobzhansky's more well-known collaborative work on the microgeographic races of the plant *Linanthus parryae* with systematic botanist Carl Epling, was dominated by concerns stemming from general patterns of evolution (in this case Wrightian evolution) rather than a genuine interest in plant evolution.[37] Dobzhansky thus held little real interest in plants, especially if their evolutionary processes seemed to contradict *Drosophila* or the general theory of evolution he had derived with Wright's assistance. He did, however, recognize the importance of their inclusion within a universal genetical and evolutionary theory and therefore followed the work of plant geneticists and evolutionists closely, drawing from plant examples to support his theory when he could. He also needed knowledge of the distribution patterns of plants which could potentially provide information of his own insect species. The life-history and natural history of *Drosophila*, for instance, was closely linked ecologically to plant life. Dobzhansky thus actively enrolled the assistance of collaborators like Epling to provide him with ecological and geographic data, and Stebbins, to sort through mechanisms like polyploidy and apomixis in order to support Dobzhansky's general theory. As a result of Dobzhansky's proximity, botanists like Stebbins, but also

[36] Anderson viewed introgressive hybridization, which involved the exchange of genetic material between species, as a creative force in evolution. See Kleinman 1999 and Smocovitis 1988 for more discussion on Edgar Anderson.

[37] Dobzhansky consulted heavily with Wright on the data that he and Epling had collected on *Linanthus.* See for instance, Letter to Sewall Wright dated October 30, 1941. Sewall Wright Papers, Series I. See also Provine 1986. Dobzhansky did, however, produce one of the classical papers in tropical botany on the strangler trees with collaborator J. Murça Pires. See Dobzhansky and Murça Pires 1954.

Epling, grew not only to understand, but also to contribute to the fund of knowledge accumulating on *Drosophila* evolution. But although Epling and Stebbins were willing to 'talk' *Drosophila* evolution with Dobzhansky who in turn was willing to 'talk' plant evolution with them, it was usually a conversation louder on one side. Dobzhansky rarely gave a central place to phenomena that he considered unique to plants.

Keeping Up with Dobzhansky: Plant and Animal Evolution

Stebbins responded to Dobzhansky's constant urgings to reconcile plant and animal evolution in the early 1940s.[38] Keeping up with Dobzhansky and the *Drosophila* program was a challenge he took up with especial zeal. The need to teach an evolution course at the College of Agriculture also continued to be a strong reason for Stebbins's broadening of interests. An examination of successive outlines of this course provides an excellent source for tracing Stebbins's intellectual development during the 'dynamic phase of evolution' (his own term) in the late 1930s and 1940s. Sequential changes of readings over the years reveals him discarding older books on evolution like De Vries and Morgan, for example, in favor of shorter articles and monographs especially by plant evolutionists like Anderson, Epling and the Carnegie team of Clausen, Keck and Hiesey.[39] The structure of the course also changed successively from a rather conventional chronological and historical organization to one dealing with specific issues of concern to evolutionists in the 1940s: variation patterns, factors responsible for variation, adaptation and selection, the structure and dynamics of populations, recombination and genetic systems, isolation and the origin of species, polyploidy and apomixis, and rates and trends in evolution.[40] The structure of the course, in fact, eventually served as the structure for his 1950 book *Variation and Evolution in Plants*.

Most importantly, Dobzhansky's book became increasingly prominent in these successive lecture outlines in the 1940s, especially after the new edition of 1941, which included more discussion of plant evolution. With each year, Dobzhansky's book (in the revised second edition) came to occupy a more central role in the course, until in 1948 it was promi-

[38] Dobzhansky's way of 'pushing' and 'urging' his friends and colleagues was noted by Stebbins. Oral History Interview, Number III, 1987.

[39] The lecture outlines begin in 1940 and end in 1949. The outlines for 1943, 1944 are missing.

[40] Document titled: Genetics 103. Spring Semester, 1948. Outline of Lectures and Reading. Box 13, Stebbins Jr. Papers.

nently designated 'textbook for the course', and headed the top of the list for general references. Other general references at the top of the list included Ernst Mayr's *Systematics and the Origin of Species*, and Julian Huxley's *Evolution: The Modern Synthesis*.[41] Overall, the lecture outlines indicated a marked shift in the goals of the course, from a teaching-oriented survey to an in-depth advanced seminar of major topics in evolutionary studies.

Concurrent with the apparently increasing confidence expressed in his teaching of evolution, Stebbins began to integrate this literature actively within his own publications. With a profound knowledge of genetics, systematics, phytogeography, an extensive knowledge of paleobotany (learned with the help of his Berkeley colleague, Ralph Chaney [1890-1971], and as one of the few botanists closely following Dobzhansky's GNP work on *Drosophila*, Stebbins began to emerge as one of the few individuals integrating perspectives from these traditionally disparate areas of botanical science. To be sure, there were other botanists at similar stages of their careers turning to the same critical problems, but none seemed to cast their net so far into the animal side of evolution in order to search for a genuine unified theory of evolution. Much more so than for Anderson, and especially Clausen, Keck and Hiesey – who were more narrowly focused on plant evolution – Stebbins sought a generalizable and universal theory of evolution that would unify botany and zoology. Epling, whose knowledge of animal evolution probably exceeded that of Stebbins, had moved too far in the direction of *Drosophila* evolution, making it his primary area of research after 1940 and largely abandoning efforts to create a coherent theory of plant evolution. None, furthermore, taught a general course of evolution that required them to be up to date with animal evolution.

In the early 1940s, Stebbins placed himself squarely in the center of the crucial discussions among evolutionists over differences between animal and plant evolution. In a series of correspondence-like exchanges over comparative rates of evolution, zoologists, botanists, geneticists and paleontologists sought to reconcile differences through 'discussion' bulletins edited, mimeographed and then sent to interested members through the National Research Council-backed Committee on Common Problems of Genetics, Paleontology and Systematics. With Ernst Mayr as editor, the first series of letter exchanges were launched by Dobzhansky requesting data from botanists on evolutionary rates in

[41] Also included were three articles by: Dobzhansky 1942; Huxley 1945; Simpson 1947.

the plant fossil record.[42] A second letter from Dobzhansky, who admitted playing 'devil's advocate' in the hope that it 'may improve the mutual understanding between zoologists and botanists,' went further in provoking discussion, especially from botanists by requesting examples of plants that met his criteria for what 'a zoologist would call a normal method of species formation'.[43] Babcock quickly responded that *Crepis* met all the criteria that Dobzhansky had requested (it had been evolving 'progressively' from the early Miocene, the main evolutionary features of this process being comparable to animals; its most 'primitive' features were in older species, while its most 'advanced' features were to be found in comparatively young species; and numerous polytypic species existed that appeared to be undergoing speciation), and Stebbins offered a lengthy explanation for evolution in plants as compared to evolution in animals.[44] In yet another exchange requesting information on mutation rates in *Drosophila* from Dobzhansky and on whether or not rates of evolution in nature are more affected by internal or genetic influences than by external background influences, Stebbins reveals the extent to which his teaching of evolution at Berkeley had encouraged him to learn to 'talk' *Drosophila* in addition to 'talking' plants.[45]

In 1944, furthermore, Stebbins was quick to defend Dobzhansky and Epling's recent pathbreaking monograph on *Drosophila pseudoobscura*, the final section (by Epling) of which drew inferences from plant evolution to expand the understanding of the evolutionary history of *Drosophila.* Eplings's portion of the monograph had been criticized by Ernst Mayr in a *Science* review as having contradictions that probably resulted from the inferential method used to connect plant evolutionary history with *Drosophila* evolutionary history (Dobzhansky and Epling 1944; Mayr 1944, 11-12). Stebbins closed his letter of defense of Epling with the following challenge to Mayr: 'If you accept as valid the evidence for evolutionary divergence from the modern distribution of plant groups, but reject any interpretation of a causal relation between distributional patterns of plants and similar or identical ones of animals

[42] Theodosius Dobzhansky, letter to Ralph Chaney, February 5, 1944. Bulletin no. 1, May 15, 1944. Committee on Common Problems.

[43] Theodosius Dobzhansky, letter to Ralph Chaney, April 14, 1944. Bulletin no. 1, May 15, 1944. Committee on Common Problems. Quotations from page 10 and 9.

[44] G. Ledyard Stebbins Jr., letter to Theodosius Dobzhansky, May 1, 1944. Bulletin no. 1, May 15, 1944. Committee on Common Problems.

[45] G. Ledyard Stebbins Jr., letter to Theodosius Dobzhansky, undated. Bulletin no. 3, Sept. 25, 1944. Committee on Common Problems. Stebbins began the letter by referring to the fact the question came up in his class.

such as *Drosophila*, can you explain why, and what substitute interpretation or interpretations you have to offer? It seems to me that the more nearly we can understand the relationship, if any, between the distribution patterns of plants and those of animals, the firmer will be our basis for the interpretation of distributional evidence for evolution as a whole'.[46] Stebbins's defense and explication of Epling's closing section of the Dobzhansky and Epling monograph soon appeared in published form in 1945 in the botanical journal *Lloydia*, and was the first of many synthetic and interpretive papers that he began to publish drawing not only upon his immediate research, but from his wide knowledge of the growing literature on *both* plant and animal evolution that was growing in the 1940s (Stebbins 1945).

The Jesup Lectures and the Solidification of a Friendship: 1946-1970

According to Stebbins the intense interactions that took place in Mather were responsible in part for the pivotal turn in his career: the invitation to give the Jesup Lectures, and with it the contract to publish the lectures in book form as part of the well-known Columbia Biological Series. He believed that it was at Dobzhansky's suggestion that L.C. Dunn (1893-1974), the geneticist who was then chair of the Zoology department at Columbia University, along with the Board of Regents, invited him to deliver the lectures in the fall of 1946. The invitation had come in the spring, shortly before March of 1946.[47] He was not the first botanist so honored; Edgar Anderson had given the Jesup Lectures with Ernst Mayr in 1941. Though Mayr had written up his lectures into *Systematics and the Origin of Species. From the Perspective of a Zoologist* in 1942, Anderson failed to turn his set of the lectures into book form.[48] The perspective of the botanist had been missing from the series, therefore, and Stebbins was to step in to fill in the gap.

Stebbins eagerly accepted the invitation, and threw himself into the preparation of his lectures. The voracious reading for Genetics 103, the

[46] G. Ledyard Stebbins, Jr., letter to Ernst Mayr, July 25, 1944. Bulletin no. 4, November 13, 1944. Committee on Common Problems. Quotation on page 3.

[47] Robert G. Sproul, letter to G. Ledyard Stebbins Jr., March 5, 1946. Family scrapbook, in the possession of G. Ledyard Stebbins, Jr.

[48] Reasons for Anderson's failure to deliver the lectures are unclear. Kim Kleinman offers a novel explanation in 'His Own Synthesis' (Kleinman 1999). According to Kleinman, Anderson was too focused on corn work at the time. Another possibility is that Anderson was unable to complete larger projects, in part the outcome of instability as a result of bipolar disorder. See Smocovitis 1988. It is also possible that the lectures became his 1949 book *Introgressive Hybridization* (Anderson 1949).

lectures for that course, and the encouragement and support of Dobzhansky paid off admirably. In the fall of 1946 Stebbins left for New York to deliver the lectures. Between October 15 and November 26, Stebbins delivered six lectures as part of the series, all in room 601 of Schermerhorn Hall, the building which had housed Morgan's famous 'fly room' some twenty years before.[49]

The period he stayed in New York to deliver the lectures helped to solidify the bond between Dobzhansky and Stebbins further. Dobzhansky and his wife Natasha insisted that Stebbins stay in their apartment during his lectureship. Stebbins accepted their invitation, which he viewed as an 'exceptional honor'. He vividly recalled how the proximity to Dobzhansky during his stay, along with the 'endless discussions' they enjoyed walking to campus daily, helped to hone his thinking about evolution. Dobzhansky also introduced him to friends and acquaintances in the area like John Moore, then at Barnard College, and the biochemist Alfred Mirsky. On weekends, Dobzhansky took Stebbins to Cold Spring Harbor, where he was introduced to geneticist Milislav Demerec (1895-1966) then turning to microbial genetics. Overall, the stay served to widen appreciably Stebbins's understanding of even newer developments in evolution (Stebbins 1995). Dobzhansky, in turn, was delighted with the lectures that Stebbins was presenting and wrote glowing reports to his Columbia colleague Dunn, who was traveling at the time of the lectures: 'In my opinion he [Stebbins] has done an excellent job. The attendance is keeping up, and there is enough discussion. Now we shall look forward to his book, which is in the final draft now. Knowing him, thereis[sic] no doubt in that the final draft will come in due time.'[50]

Returning from his lectures, Stebbins threw himself into the revisions, which assimilated even more recent literature in both plant evolution and animal evolution. He took approximately two years to complete the final draft. According to Stebbins, it was sent off at the end of 1948 and was published in 1950.[51] The longest and last book of the Columbia Biological Series, the publication outlet for the Jesup Lectures, was well received. Reviews praised it widely and at least one recognized him as a 'disciple of Dobzhansky' (Baker 1950; Anderson

[49] Jesup Lecture announcement and invitation. Family scrapbook, in the possession of G. Ledyard Stebbins Jr.

[50] The final sentence may have cryptically referred to Anderson's failure to complete his manuscript. Theodosius Dobzhansky, letter to L.C. Dunn, November 25, 1946. Dunn Papers, folder titled Theodosius Dobzhansky, 1946-1947.

[51] Oral History Interview, Number IVa , 1987.

1950; Epling 1950). Yet another hailed the appearance of the fourth volume of the Columbia Biological Series by stating that the book 'maintains its standards and makes another major contribution to the literature which deals with the fundamental problems in evolution' (Zirkle 1951, 83-84). Stebbins himself became closely identified with the authors of the other evolution books in the Columbia Biological Series. When the 'evolutionary synthesis' was assessed as a historical event in 1974, Ledyard Stebbins was ranked alongside Dobzhansky, G.G. Simpson, and Ernst Mayr as one the 'architects' of the evolutionary synthesis. He was the one who is credited with 'bringing botany into the synthetic theory of evolution'.[52]

Fortunately, Dobzhansky's immediate reaction to *Variation and Evolution in Plants* is recorded. He wrote:

> 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-root botanical systematics![53]

From the fall of 1946 on, Dobzhansky and Stebbins had become special friends. As their friendship had grown, so too had their views of evolution come to resemble each other more closely. Their close friendship continued through the 1950s, even though they had major changes in their lives. In 1950 Stebbins accepted the offer to move to the new campus of the University of California at Davis, where he subsequently was instrumental in building the genetics department.[54] Dobzhansky stayed at Columbia until 1962, when he moved to the Rockefeller University. In the 1950s Dobzhansky visited Mather less frequently as he shifted his interest to the tropical species *Drosophila willistonii*, which took him to places like Brazil, Ecuador, and Colombia, but where he still remembered his botanical friends in the US.[55] There were also occa-

[52] Mayr and Provine 1980; see also the correspondence about, and the transcripts of the two 1974 workshops for the evolutionary synthesis organized by Mayr located in the Library of the American Philosophical Society.

[53] Theodosius Dobzhansky, letter to G. Ledyard Stebbins Jr., August 27, 1950. In the author's possession.

[54] See the brief history of the department in Stadtman and the Centennial Publications Staff, 1968, 175-176.

[55] Dobzhansky occasionally dropped notes to his friend during these travels. Box 13, Stebbins Jr. Papers. And see where Dobzhansky wished for his friends Epling and Stebbins when he saw the mysterious flora of the Bahian caatinga in Letter titled 'Blind Alleys of Bahia,' dated São Paulo, March 11, 1949, pp. 52-60 (Glass 1980, 57).

sional visits to Mather, shared conversations at meetings like the International Congress of Genetics in Montreal in 1958,[56] and the numerous meetings prompted by the centennial of the publication of Darwin's *Origin* in 1959.[57] In 1958 Dobzhansky and Stebbins even collaborated on a series of television lectures on genetics.[58] By 1960, in fact, their names were linked in increasing frequency, with Stebbins taking on the role of the leading botanist in evolutionary biology. Dobzhansky, in fact, invited his friend, 'The greatest authority of Plant Evolution, and one of the greatest on any kind of evolution', to contribute to the first volume in the new series *Evolutionary Biology*.[59]

In 1961, just after he had accepted the position at Rockefeller University, Dobzhansky received an invitation from Stebbins to come to Davis. Dobzhansky courteously responded to the invitation with the surprising statement that 'my roots go much deeper in the stone and asphalt soil of Manhattan'. He declined the offer also because of commitments to his collaborators and students, many of whom would have been 'orphaned' in the move. He closed with a friendly thought: 'Let me say this quite frankly-at the age of 62 I feared nobody would consider me a fit candidate for a job. And with you I felt also something else - I felt a warmth of personal welcome which I shall never forget and for which I am deeply thankful to you. Though living in different cities, I can only hope that we shall maintain this friendship as long as we live'.[60]

Dobzhansky and Stebbins at Davis, 1970-1975.

Dobzhansky's wish was granted: at the time of his death, Dobzhansky and Stebbins were at their closest, having shared their science, lives and memories of earlier times in the same city and on the same campus. In the late 1960s as Dobzhansky was nearing retirement at the Rockefeller Institute, he feared that his laboratory space was to be significantly reduced. This would have cut his research efforts considerably and with

[56] Stebbins recounts Dobzhansky's reaction to H.J. Muller's address which criticized Dobzhansky's 'balance theory' in favor of Muller's 'classical theory' (Stebbins 1995, 7-13).

[57] See the correspondence between Dobzhansky and Stebbins for note of their interactions in the late 1950s. Box 13, Stebbins, Jr. Papers.

[58] G. Ledyard Stebbins Jr., letter to Theodosius Dobzhansky, February 13, 1959; G. Ledyard Stebbins Jr., letter to Theodosius Dobzhansky, April 2, 1958. Box 13, Stebbins Jr. Papers.

[59] Theodosius Dobzhansky, letter to G. Ledyard Stebbins Jr., May 21, 1965. Box 13, Stebbins Jr. Papers.

[60] Theodosius Dobzhansky, letter to G. Ledyard Stebbins Jr., December 22, 1961, Box 13, Stebbins Jr. Papers.

the death of his wife Natasha in 1969, he decided to consider other locations for his work. According to one account by Howard Levene, it was Dobzhansky's old friend, Michael Lerner who suggested to Dobzhansky that he consider Davis as a permanent home. The department of genetics there was 'having a search' for an associate level geneticist, and Lerner suggested that Dobzhansky's protégé, Francisco Ayala, could fill the slot, bringing Dobzhansky and other collaborators to Davis (Levene 1995). Documents in archives and from oral history interviews actually point to efforts to bring Dobzhansky to the Davis campus as early as February 11, 1969, when Stebbins arranged a visiting professorship to last three months for Dobzhansky as part of an NIH Training Grant in Genetics.[61] One letter of exchange between them, written just one week after the loss of Natasha hints at Dobzhansky's grief.[62] This, and the fact that Dobzhansky was increasingly facing both isolation and budget cuts at the Rockefeller, which had few organismic biologists, were likely strong motivators for his decision to move to Davis in 1970.[63] He enthusiastically wrote to Stebbins in January 22, 1970:

> In 10 days I shall be 'emeritus', which is a sad but inevitable turning point in one's life. Of course, the prospect of California pleases me greatly, I know the attractions of the West, in fact all these years Natasha and myself felt 'spiritual Westerners'. And yours and Barbara's invitation to stay with you is most kind, and of course, is accepted.[64]

Backed by the chair of the genetics department, Robert Allard, Stebbins helped convince the administration to hire Francisco Ayala and Dobzhansky together (Dobzhansky as 'Adjunct Professor of Genetics'). The two arrived in 1971. In addition to inviting Dobzhansky to groups like the Biosystematists, student seminars, and introducing him to colleagues like philosopher Marjorie Grene,[65] Stebbins tried to make Dobzhansky feel welcome on the Davis campus. Correspondence available for this time reveals the arrangements made by Stebbins with Dobzhansky and Ayala to ease Dobzhansky, diagnosed with leukemia in

[61] G. Ledyard Stebbins Jr., letter to Th. Dobzhansky, February 11, 1969. Stebbins Jr. Papers. Oral History Interview, Number III, 1987.

[62] Theodosius Dobzhansky, letter to G. Ledyard Stebbins Jr., March 2, 1969. Box 13, Stebbins Jr. Papers.

[63] Francisco Ayala, letter to Howard Levene, April 5, 1970. Box 13, Stebbins Jr. Papers.

[64] Theodosius Dobzhansky, letter to G. Ledyard Stebbins, Jr., June 22, 1970. Family scrapbook, in the possession of G. Ledyard Stebbins, Jr.

[65] G. Ledyard Stebbins Jr., letter to Theodosius Dobzhansky, March 10, 1971; Theodosius Dobzhansky, letter to G. Ledyard Stebbins, Jr., March 12, 1971; G. Ledyard Stebbins Jr., letter to Theodosius Dobzhansky, March 16, 1977. Box 13, Stebbins Jr. Papers.

1968, through the difficult process of moving. Stebbins and his wife Barbara were especially supportive of Dobzhansky, inviting him to stay in their home and helping with arrangements while his new – and his first – home, a duplex, was being built. Barbara warmed to Dobzhansky, becoming (according to Stebbins) something of a surrogate for Natasha, and both discovered a shared taste for Italian arts. In appreciation for the hospitality, Dobzhansky gave Barbara and Ledyard a canoe to be used at their cabin on Wright's Lake. Barbara and Ledyard named the canoe 'Doby' in honor of their friend and continued to joke affectionately about 'paddling Doby', until Barbara's death in 1993'.[66]

The night before Dobzhansky died he had been to dinner at the Stebbins's. Shortly before leaving for the night he turned to Barbara and told her 'I don't think it will be long now'.[67] Dobzhansky died the next morning of heart failure in Francisco Ayala's car on the way to hospital emergency; it was December 18, 1975. His ashes were eventually buried near Natasha's close to a granite boulder in Mather, just by a favored site Dobzhansky and Stebbins frequented on horseback.

The loss was felt deeply by the numerous students, collaborators, and friends, and especially so by Stebbins, who participated in numerous projects including administering the Dobzhansky Memorial Prize of the Society for the Study of Evolution,[68] and contributing to *Festschrifts* and conferences in Dobzhansky's honor. Stebbins mimeographed a testimonial titled 'Theodosius Dobzhansky's Last Scientific Discussion', that he distributed to mutual friends and colleagues. Stebbins addressed the 'Friends of Dobzhansky':

> We'll all have memories of scientific wisdom, unassuming personality and kindliness to all of us on an equal basis that was so characteristic of our departed friend and leader in the field of evolution. Through the years, he has sent us his impressions of science and life in many countries of the world in the form of mimeographed round robin letters. Perhaps you have been keeping a file of these. If so, and even if not, you may wish to share with me his last scientific discussion. To me,

[66] Oral History Interview, Number III, 1987. When I visited the Stebbins home in 1988, Barbara Stebbins showed me a carefully packed container holding yet another gift from Dobzhansky, an Italian ceramic tea service.

[67] Oral History Interview, Number III; and see the mimeographed memorial Stebbins sent to mutual friends and colleagues: 'Theodosius Dobzhansky's Last Scientific Discussion'. Cain Papers, Folder titled G. Ledyard Stebbins, Series I.

[68] Document titled 'Resolution passed by the Council of the Society for the Study of Evolution, May 30, 1976. Adopted by Society, May 31, 1976'. Document by Howard Levene with extract of letter by R.C. Lewontin; and see Letter from Howard Levene to G. Ledyard Stebbins Jr. inviting him to the committee to administer the prize. Stebbins was instrumental in informing botanical journals of the new award. These documents are in Box 13, Stebbins Jr. Papers.

> it is the most fitting epitaph that I can imagine for one of the greatest scientists and humanists of our time.[69]

At the time of his death, Dobzhansky had recently completed his portion of a multi-authored book on *Evolution,* written with Francisco Ayala, James Valentine, and G. Ledyard Stebbins. Appearing in 1977, it was their only collaboration resulting in a published work (Dobzhansky, Ayala, Stebbins and Valentine 1977).

Dobzhansky and Stebbins: Analytical Perspective and Closing Thoughts

Dobzhansky thus went to the grave as a very special friend, if not a kind of 'hero' to Stebbins. Throughout all of his oral history interviews and formal conversations, Stebbins never once spoke ill of his friend. Dobzhansky regarded 'his friend Stebbins' favorably too, but there is little indication that the feelings were fully reciprocated. The power dynamic on the personal scale thus appears slanted to one side. Can the same relationship be said to extend to their science?

As this historical reconstruction has suggested, Stebbins followed Dobzhansky's 'lead' in a number of ways. Beginning with the publication of *Genetics and the Origin of Species* in 1937, which Stebbins found exciting for offering the possibility of understanding mechanisms of speciation at a genetic level, Stebbins began applying Dobzhansky's insights to his own work on the genus *Crepis.* But the book fundamentally did not speak *sufficiently* to problems of plant evolution for the botanist. Dobzhansky's shift to the GNP series and the move towards a more adaptationist approach to evolution was critical to further drawing in Stebbins because they seemed more compatible with observations Stebbins had been making in the genus *Crepis* and because Stebbins favored more adaptive explanations for divergence. Stebbins actively sought the insights, advice, and company of Dobzhansky during the summers at Mather, which further intensified their relationship. Having recognized the potential of Stebbins's contribution, and needing a botanical perspective to add to the Jesup Lectures (Anderson having failed to complete his manuscript of the 1941 Lectures with Mayr), Dobzhansky was instrumental to inviting Stebbins to give the Jesup lectures. The duration of the lectures saw the further intensification of the

[69] Two-page mimeographed document by G. Ledyard Stebbins. Cain Papers, Series I. Folder titled G. Ledyard Stebbins.

relationship between the two, which became apparent in the book version of the Lectures published as *Variation and Evolution in Plants.* Without doubt the book was *the* most important product that resulted from the Stebbins-Dobzhansky interaction.

But it is also important to note that Stebbins was *already* taking an evolutionary direction well before his contact with Dobzhansky. His research program on *Crepis*, for instance, had fueled his interest in understanding the genetical mechanisms for evolutionary change, and his discussions with like-minded scientists in groups like Genetics Associated, the Biosystematists in the Bay area, and with his botanical colleagues Anderson, Epling, and the Carnegie team of Clausen, Keck, and Hiesey had contributed greatly to his pending synthesis of plant evolution. Most important in his intellectual development was his teaching of the evolution course at Berkeley, which gave him the opportunity to read widely in order to synthesize animal evolution with plant evolution. Thus, although in some respects he followed Dobzhansky's 'leadership' role in the evolutionary synthesis, Stebbins was also taking his own direction, quite independently of Dobzhansky.

As the historical reconstruction has also suggested, the relationship was not slanted completely to one side: Dobzhansky actively sought understanding of plant evolution both in supporting the theoretical framework articulated in *Genetics and the Origin of Species*, but also as part of his understanding of the geographic variation patterns of *Drosophila pseudoobscura.* For this reason he sought Epling's direct aid, and through Epling also became closer to Stebbins. Dobzhansky's growing knowledge of plant evolution, the result of increasing interaction with botanists, is apparent in the 1941 edition of *Genetics and the Origin of Species.* Although he did not give the highest priority to understanding plant evolution, he sought to understand mechanisms of evolution operating in plants both in his brief study of introgressive hybridization in the manzanitas, and his more significant project on *Linanthus,* on which he collaborated with Epling. Both these studies were used to support the theoretical commitments that he was making from his interaction with Sewall Wright.

An additional factor that helped bring Dobzhansky and Stebbins together was the fact that both sought a general theory of evolution. This goal to generalize and to formulate a unified theory of evolution in turn allowed them to adjust to a range of study organisms that they studied at the most ultimate level of evolution available to them, namely, the chromosomes. Later in the 1960s, when molecular techniques became available to understand evolution at the genic level, both took advantage of the new perspective and adjusted their research accordingly.

The institutional location in the Bay area, which brought Stebbins in contact with mutual friends like Lerner, as well as other visitors to the Bay area like Epling and Anderson, and the Biosystematists and Genetics Associated also facilitated interaction. Critically important too, was the fact that both Dobzhansky and Stebbins collected California fauna and flora respectively, and frequented the same sites at Mather. For Stebbins and Dobzhansky, as for Epling and Clausen, Keck and Hiesey, Mather in the 1940s could in fact be viewed as a cross between a 'natural laboratory', 'experimental garden' and an 'evolutionary think-tank'. Dobzhansky and Stebbins also had personal qualities and a 'chemistry' that drew them together. Both had dynamic, energetic personalities, with an infectious enthusiasm towards work and life. Both also had an almost obsessive, single-minded approach to work. Although they came from vastly different personal backgrounds (Stebbins, the son of a wealthy New York businessman, Dobzhansky a refugee from Stalinist Russia), they shared similar liberal politics, and a comparable view of 'biology and Man'.[70] In the late 1940s and 1950s, for instance, Dobzhansky and Stebbins were two of the most vocal critics of Lysenko's assault on genetics in the Soviet Union. And although they came from vastly different religious backgrounds (Stebbins, an Episcopalian-turned-Unitarian and self-described 'agnostic', Dobzhansky a devout member of the Russian Orthodox Church), both made the cover stories of *The American Biology Teacher* in the mid-1970s with their defense of evolution in the wake of 'scientific creationism'. But both also had a strong sense of self-presence and possessed what we might call 'strong personalities'; both liked to have their way and that made conflict between them always a possibility. This rarely happened, however, because they appeared to respect each other's areas of expertise albeit with Stebbins showing the greater tendency to defer to Dobzhansky.

Importantly, there were few occasions for conflict because they never actually collaborated on research projects. Unlike Dobzhansky and Epling, who eventually broke with each other over a violent difference of opinion over interpretation on *Drosophila pseudoobscura* data in 1953, Dobzhansky and Stebbins never really tried to integrate their areas of immediate research, but instead, focused on integrating their synthetic, large-scale interpretive studies on general evolution. Thus, while Dobzhansky and Stebbins could occasionally disagree on points of interpretation, for example, on the relative importance of introgression and the presence of reticulating evolution in general evolution, such disagreement could easily be understood as a difference of opinion

[70] See the suite of essays on Dobzhansky's worldview (Adams 1994).

owing to their differing organismic systems. Both had well-defined niches in the social landscape of evolutionary studies, especially by the 1950s. Any differences could be interpreted as nearly always being *relative* with respect to their organismic system. Dobzhansky and Stebbins were thus spared of the close negotiations over details that come with data collection, interpretation, and presentation in a full-blown scientific or research collaboration.

Finally, the fact that they were both evolutionary cytogeneticists crossing into field-oriented studies helped draw them together, as did the fact that their organismic systems, plants and insects, were dependent on each other: from a botanical standpoint, insect evolution is closely linked to plant evolution, given their close ecological association. The stunning early work demonstrating coevolution, it will be recalled, drew on such insect-plant interactions (Ehrlich and Raven 1964). Furthermore, as the exchange between Stebbins and Mayr over Mayr's criticism of Epling's portion of Dobzhansky and Epling's 1944 monograph shows, the dividing line could easily form between insect and plant workers on one side, and bird and mammal workers on the other. Dobzhansky's Russian background which stressed ecological relationships like those seen in insect-plant interactions may have in part contributed to his more ecumenical evolutionary view. It was certainly ecumenical when compared to the other zoologists of the synthesis, Simpson and Mayr, who took little interest in the botanical side of evolution. In this respect, the pairing of Mayr, a zoologist, with Anderson, a botanist, (whose personalities were fundamentally at odds with each other) for the Jesup Lectures may have produced an incompatible union that in part contributed to Anderson's failure to complete a book-length manuscript. It certainly failed to create a synthesis between animal and plant evolution in 1941. This failure may in some manner also help to explain Mayr's sense that botany was 'delayed' in entering the wider synthesis;[71] if so, then the possibility exists that Mayr – indirectly – contributed to this delay. But as this historical reconstruction has shown, botanists were actively engaged in the synthetic project throughout the period of the synthesis; it was not through botanists 'failure' or inadequacy that the botanical work of the synthesis period was the last of the 'synthesis' books to appear. The sheer volume of material to assimilate may also have contributed to the 'delay'. Certainly *Variation and Evolution in Plants* was the densest of all the books in the Columbia Biological Series.

What general conclusions then, can we draw from the Dobzhansky-Stebbins 'union', and their conversations over plant and animal evolu-

[71] See Ernst Mayr's reflections on botany and the synthesis in Mayr and Provine 1980.

tion during the period of evolutionary synthesis? For one thing, the evolutionary synthesis required the expertise of a vast number of workers, working on different organismic systems which frequently contradicted each other. Stebbins may have felt Dobzhansky's 'charismatic influence', or even 'Messianic influence', which played a vital role in producing *Variation and Evolution in Plants*. But it is important to note that Stebbins was also taking an evolutionary direction on his own apart from Dobzhansky. Dobzhansky in turn, received powerful validation for his own theoretical arguments from his conversations with Stebbins, but also engaged in limited research with plants himself. The direction of influence was thus not 'one way', but was multi-directional and involved other factors including fundamental commitments to science, compatible personalities, work styles, locations, and habits, and a shared network of researchers. Finally, the Dobzhansky-Stebbins interaction helps make the point once again that science is done by human beings, whose personal interactions have much to do with the way their work develops and in this case especially, the form it finally takes.[72]

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[72] For a recent example demonstrating the importance of personal interactions in shaping science see Burkhardt 2005.

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