

DESCENDED FROM DARWIN
INSIGHTS INTO THE HISTORY OF
EVOLUTIONARY STUDIES, 1900–1970

Joe Cain and Michael Ruse, Editors

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CHAPTER 4

BIOSYSTEMATICS AND THE ORIGIN OF SPECIES

EDGAR ANDERSON, W. H. CAMP, AND THE EVOLUTIONARY SYNTHESIS

Kim Kleinman

The very process of synthesis combines disparate elements into a coherent whole, making complex phenomena more comprehensible as we understand which factors are decisive and, as importantly, which ones less so. Synthesis is a powerful intellectual tool, a beacon that illuminates a wide swath of previously unrelated facts, theories, and even disciplines. In biology in the second quarter of the twentieth century, just such a synthesis between genetics and evolutionary theory flourished through the work of R. A. Fisher, Sewall Wright, J. B. S. Haldane, Theodosius Dobzhansky, Ernst Mayr, George Gaylord Simpson, and many, many others.

In addition to his crucial scientific work, Mayr made an invaluable organizational contribution through the Society for the Study of Evolution and its journal *Evolution* (Cain, 1993, 1994, 2000b; Smocovitis, 1992, 1994a, 1994b, 1996). As a historian, he continues to shape how we think about these developments (Mayr & Provine, 1980). As Mayr explains it,

The term “evolutionary synthesis” was introduced by Julian Huxley in *Evolution: The Modern Synthesis* (1942) to designate the general acceptance of two conclusions: gradual evolution can be explained in terms of small genetic changes (“mutations”) and recombination, and the ordering of this genetic variation by natural selection; and the observed evolutionary phenomena, particularly macroevolutionary processes and speciation, can be explained in a manner that is consistent with the known genetic mechanisms. (Mayr & Provine, 1980, p. 1)

Further, of all evolutionary theories, only neo-Darwinism or synthetic theory—as opposed to saltationism (evolution by sudden leaps), Geoffroyism (evolution under direct influence of the environment), orthogenesis (evolution by an organism’s built-in

tendency toward perfection or progress), or even Darwinism—combines both population thinking (an appreciation for variation as opposed to “essentialism”) and a commitment to hard inheritance (Mayr & Provine, 1980, p. 4). Forging this synthesis required “bridge builders,” geneticists who had experience with natural populations and naturalists who had absorbed the work of the geneticists.

Botany posed its own problems. Mayr identified at least two: a sharper differentiation than among zoologists between museum-herbarium workers and their counterparts doing field work and “genetic systems in plants tend to be a good deal more complicated than those of . . . animal groups,” which in turn “prevented unanimity in the adoption of a uniform species concept” (Mayr & Provine, 1980, p. 137). The result was that “in the 1930s and 1940s no botanist published a book comparable in impact to the books of Dobzhansky, Huxley, Mayr, Rensch, Simpson, or other architects of the synthesis.” It would fall to G. Ledyard Stebbins’s *Variation and Evolution in Plants* (1950) to fill that niche. And even then, in 1963, Mayr wrote, “Each of the kingdoms has its own evolutionary peculiarities and these must be worked out separately before a balanced synthesis can be attempted” (Mayr, 1963, p. v). This comment was a partial explanation of why his book of that year was titled *Animal Species and Evolution*; he, at that point, had 35 years of field and laboratory experience with animal species, but “Lacking a similar familiarity with plants, I might have come up with absurd generalizations if I tried to apply my findings to plants” (Mayr, 1963, p. v).

As illuminating as Mayr’s perspective on the synthesis is, it cast shadows, leaving some things less clear. The bright beacon washes out some of the nuances and subtleties of lived experience. Edgar Anderson, as an interested participant, used a review of Dobzhansky’s *Evolution, Genetics, and Man* to keep some of those nuances, what he called “odd noises,” on the table:

In personal conversation Professor Dobzhansky has sometimes chided scholars who, like this reviewer, cherish a Batesonian interest in those few significant facts which do not fit easily with today’s facile exposition of basic principles. At such times, he cites an old Russian proverb, warning one against “making odd noises for the benefit of future generations.” There are few such “odd noises” in this book. They are probably pretty much out of place in modern textbooks. (Anderson, 1956c)

More recently, scientists and/or historians such as Gould (1983) and Provine (1981) have noted that the synthesis “hardened” or, alternatively, “became unraveled.” Similarly, Joe Cain concluded a study of what he called “the New York Circle” of evolutionary biologists (that is, key players in the evolutionary synthesis) in the period 1936–1947 with this historiographical caution:

Just as prominence does not guarantee influence (and just as aggressive promotion does not imply hegemony), certainly influence neither requires nor ensures prominence. In highlighting the New York Circle, who is being missed? Little is written, for example, of Edgar Anderson—an experimental taxonomist working at the Missouri Botanical Garden—whose research on *Iris* was widely discussed at the time and who, with Mayr, delivered part of the 1941 Jesup Lectures. . . . Unfortunately, the prominence (and real influence) of the New York Circle may obscure a more comprehensive understanding of the synthesis period. (Cain, 1993, p. 25)

I would like to offer my own “odd noises” in an attempt to contribute to a more comprehensive understanding of the synthesis period. Within the framework of the traditional evolutionary synthesis historiography in terms of the Jesup Lectures and the volumes derived from them published by the Columbia Biological Series, I can add a bit more to the “mystery” of why Edgar Anderson did not publish the *Systematics and the Origins of Species: From the Viewpoint of a Botanist*, based on his half of the 1941 Jesup Lectures, as he was contracted to do. In doing so, I chronicle his collaboration with W. H. Camp around Camp’s 1943 paper with C. L. Gilly on “The Structure and Origin of Species” (Camp & Gilly, 1943). Anderson and Camp were just two of a host of plant scientists who under the banners of “experimental taxonomy” and “biosystematics” were synthesizing genetics, ecology, and taxonomy to answer evolutionary questions. While not seen as part of the evolutionary synthesis, they nonetheless are significant if we are to understand how scientists were working on these questions in this key period. In writing this botanical work into the history, it can also remind us that there is much plant evolution that, though comprising some “few significant facts which do not fit easily with today’s facile exposition of basic principles,” must be incorporated into any synthetic theory of evolution.

EDGAR ANDERSON’S CAREER TO 1941

By 1941, Edgar Anderson was well qualified to address the question of “Systematics and the Origin of Species from the Viewpoint of a Botanist” posed by the organizers of the Jesup Lecture series at Columbia University (Cain, 2001, 2002a). They asked Mayr and Anderson to explore that question as a follow up to the lectures by Dobzhansky in 1936, which became *Genetics and the Origin of Species* (Dobzhansky, 1937).

Anderson had received his SciD from the Bussey Institution at Harvard. There he worked particularly with E. M. East, but also W. E. Castle, Oakes Ames, and W. M. Wheeler, in what Anderson himself called “one of the most successful experiments in higher education which has yet been undertaken in this country” (Anderson, 1940, p. 117). Anderson’s cohort of classmates included Alfred Kinsey, Paul Mangelsdorf, and G. Ledyard Stebbins. East at Harvard and R. A. Emerson at Cornell trained an entire generation of maize geneticists. Though Anderson later carried out a broad interdisciplinary research into maize, quipping that he was “an authority at what was NOT known about it [corn]” (Anderson, 1968, p. 373), but his own doctoral research was on self-sterility in *Nicotiana* (flowering tobacco) hybrids (Anderson, 1924). He came to the Missouri Botanical Garden in 1922 as “Geneticist to the Garden,” with responsibilities as head of the School of Gardening and also as an assistant professor at Washington University. Near the end of his career, he noted the impact of the Garden on his career by commenting,

The main interests of my colleagues and students were in taxonomy, morphology, and physiology. I was keenly interested in natural history and the then little known Ozarks were at our back door. I taught genetics, but I explored the Ozarks with my students. They learned genetics from me, and they convinced me that I should take a serious interest in taxonomy. With them and with other colleagues and students I have studied it ever since. We really explored together much more than the Ozarks; we explored the wide

field between genetics and taxonomy, then a *terra incognita*. . . . With my students, I helped originate what is now called “biosystematics.” (Anderson, 1968, p. 373)

This work at the interface of genetics and taxonomy, the then new field of “biosystematics,” is a big part of Anderson’s synthetic contribution to evolutionary theory as well, for that reason, this paper.

His first biosystematic project was a look at the species problem in *Iris*. His 1928 paper took up the species problem concretely by looking at populations of two closely related yet distinct species of iris and allowed Anderson to test the relative importance of hybridization and mutations as sources of the variation on which natural selection works (Anderson, 1928).

Anderson determined first that *Iris versicolor* is made up of two species—a northern one with short lanceolate petals and a short ovary, which extends from New England west to northern Michigan and another which ranges from the Great Lakes to the Gulf of Mexico and up the Southern Atlantic seaboard with obovate-spatulate petals and long ovaries. By examining the specimens of Linnaeus himself and other of his contemporaries, Anderson determined the second group was in fact *Iris virginica*.

While the ranges of the two Northern blue flags (*Iris versicolor* and *I. virginica*) were fairly distinct, Anderson found some overlap in Michigan and Ontario around the Great Lakes. In his experimental plots, Anderson found the hybrids partially fertile with “slightly more than half of those [crosses] *between* the two species have” set seed. While that seed did not frequently germinate, those that did showed hybrid vigor, that is, a tendency to exceed either parent in some quality, be it size, fecundity, and so forth. Thus, Anderson was particularly interested in hybrid colonies at West St. Ignace and Engadine in Northern Michigan. At the latter location, Anderson proposed that the hybrid plants were sufficiently distinct and stable to warrant a special name, “*X Iris robusta* E. Anderson.” Further, as he puts it mildly, “There is some evidence that constant new forms might originate in this manner” (Anderson, 1928, p. 306).

Thus, Anderson set himself against the “general theory . . . held by many of the *Drosophila* workers who see in the gene mutation the unit of process, which compounded a thousandfold, results in specific differences.” Instead, he explained,

The careful investigation of these [true-breeding] hybrids [resulting from new chromosomal realignments] has strengthened the case of those who believe with Lotsy ('16) that hybridization has been an important factor in the evolution of species. Though it has not been investigated cytologically, the colony studied at Engadine [*Iris robusta* E. Anderson (*Iris versicolor* \times *I. virginica*)] is apparently composed of similar true-breeding hybrids of natural origin. While it will have to be very thoroughly investigated before it can be taken as conclusive, this apparent example of a new constant form produced by hybridization of two separate species is certainly very suggestive. (Anderson, 1928, pp. 311–312)

Thus, with this paper Anderson introduced a fresh perspective to the unfolding evolutionary discussions.

When Anderson returned in 1936 to “The Species Problem in *Iris*,” he benefited from his work in 1929–1930 at the John Innes Horticultural Institute in England (Anderson, 1936a). Under a National Research Fellowship, he was able to spend this sabbatical working with C. D. Darlington on cytogenetics, J. B. S. Haldane on genetics, and R. A. Fisher on statistics.

The *Primula* work at the “old John Innes” of which he was a part, showed that speciation could occur through amphidiploidy in hybrids. *Primula kewensis* is typically a highly sterile hybrid of *P. floribunda* and *P. verticillata*. Each parent has 9 chromosomes as does the sterile form of *P. kewensis*. However, the occasional fertile flowers turned out to have 18 chromosomes, the result, Anderson explained, of “an exceptional nuclear division in the inflorescence of the sterile hybrid . . . not accompanied by a cell division and a sector arose in which the entire chromosome complement had been duplicated” (Anderson, 1936a, p. 473). Thus, while the sterile hybrid would have 9 chromosomes each from *P. floribunda* and *P. verticillata* and therefore be unable to reproduce as the unlike chromosomes could not pair, the fertile, true-breeding hybrid (i.e., an amphidiploid) had two full sets of chromosomes from each parent.

For Anderson, here was a possible explanation to his conclusion that the slow accumulation of individual differences could not account for speciation in his *Iris* species, that the differences between species are of an entirely different order from the differences between individuals. Thus, his 1936 *Iris* paper explored the hypothesis that *Iris versicolor* was resulted from a cross between *I. virginica* and *I. setosa* from Alaska. Among the compelling evidence he adduces is that *I. virginica* had 70 to 72 chromosomes and *I. setosa* has 38 while, fittingly, *I. versicolor* has 108. As a result Anderson estimated that morphologically *I. versicolor* was approximately two-thirds *I. virginica*, one-third *I. setosa* (Anderson, 1936a, pp. 478–482 and the remarkable plate 23). As he put it,

Iris versicolor often reminded one of *Iris virginica*, but *Iris virginica* never reminded one of *Iris versicolor*. If on the above hypothesis, *Iris versicolor* is indeed *Iris virginica* plus something else, then the relationship should be different in one direction from what it is in the other. (Anderson, 1936a, pp. 481–482)

The difference in chromosome contribution from the different parents provided a tidy explanation of this impression borne of Anderson’s extensive observations of populations of these plants.

Another important connection Anderson made through his *Iris* work and his year at the John Innes Horticultural Institution was his friendship with R. A. Fisher,¹ who gratefully acknowledged Anderson and his *Iris* data in his 1936 paper “The Use of Multiple Measurements in Taxonomic Problems” (Fisher, 1936). Here Fisher developed his linear discriminant function and turned it to confirming Anderson’s views on the hybrid origin of *Iris versicolor*. Fisher’s influential and powerful mathematical tool was yet another outgrowth of Anderson’s first major research project.

Following on this work with *Iris*, Anderson embarked on a synthetic multidisciplinary examination of *Tradescantia*. Between 1934 and 1938, he published eight articles² on the spiderworts with such collaborators as cytologist Karl Sax and taxonomist Robert Woodson. One with Leslie Hubricht marked the first use of the term “introgressive hybridization” to describe the role of backcrosses from hybridizations as a source, potentially as significant as mutations, for the genetic variability on which natural selection could work (Anderson & Hubricht, 1938).

It was just such work that qualified Anderson to share the 1941 Jesup Lectures with Ernst Mayr to discuss “Systematics and the Origin of Species” from their respective disciplinary perspectives.

THE 1941 JESUP LECTURES AND THEIR AFTERMATH

Ernst Mayr has recounted that

Edgar Anderson gave two lectures and I also gave two. We did not consult each other prior to the lectures. Anderson, if I recall correctly, presented some very specific cases. In particular, he compared two very similar species of bellworts (*Uvularia grandiflora* and *U. perfoliata*) and showed how different they were in everything, nevertheless. The other lecture he may have devoted to his irises. I have forgotten. Even though he was committed by contract and the receipt of a \$500 fee to submit a manuscript, he never did.³

What happened to Anderson's lecture notes, draft chapters, or any other related material is an obviously tantalizing question for historians of the evolutionary synthesis. In his introduction to the 1999 edition of *Systematics and the Origin of Species: From the Viewpoint of a Zoologist*, Mayr proposes that "Anderson became ill" after they had begun working on a joint volume on speciation for the Columbia University Press (Mayr, 1999, p. xvii; also Kohler, 2002, p. 265). In his 1995 letter to me, Mayr was even more candid: "I believe he had one of his depressions at that time."⁴

Anderson was hospitalized in the late 1950s and early 1960s for what seems to be bipolar disorder and also reported to psychologist Anne Roe, who interviewed him for *The Making of a Scientist* (Roe 1953), that he suffered a near nervous breakdown while at the Arnold Arboretum in the early 1930s.⁵

However, I do not believe that Anderson suffered these problems in the 1940s (Kleinman, 1999). Instead, he embarked on a particularly productive stage of his career as he turned his insights into hybridization as an evolutionary mechanism and plant-human interactions to advance what I called "his own synthesis," an examination of maize that combined archaeology, anthropology, agronomy, cytology, genetics, and taxonomy (at least).

Following up, though, on Mayr's recollection, one can infer which subsequent publications (Anderson & Palmer, 1935; Anderson & Whitaker, 1934), especially *Introgressive Hybridization* (Anderson, 1949), include both the research and conclusions Anderson likely presented.

In 1999, I also reported that there was but one reference to such a manuscript in the Anderson papers in the Archives of the Missouri Botanical Garden (Kleinman, 1999). In an undated letter (certainly though from later summer 1941), he wrote from Cold Spring Harbor to Garden Librarian and publications editor Nell Horner:

I stayed until the last possible moment to see Dr. Dobzhansky and go over the two chapters of the forthcoming book which I have written this summer. He was dallying with our own Eppie [Carl Epling] and a broken rib and has been variously due at odd moments since the 27th of August. However he came and I had a long confab with him and an evening with him and [W. H.] Camp of the NYBG and now am putting things into boxes with a vim.⁶

In the Camp Papers at the New York Botanical Garden are his letters with Anderson, which shed light on Anderson's thinking about his Jesup Lectures manuscript. Briefly, he gave a close reading of a draft of Camp's 1943 paper with C. L. Gilly, "The

Structure and Origin of Species,”⁷ and contributed significantly to the section on “Allopolyploidism.” Most interestingly, he raised, both with Camp and then Dobzhansky, the possibility of a joint publication that would incorporate their paper with his Jesup materials.

AN ANDERSON-CAMP COLLABORATION?

On March 20, 1942, Anderson wrote Camp a letter commenting on a draft of what would become “Structure and Origin of Species.” He evidently sent back an annotated copy of the first section with the promise of more to follow and offers the general suggestion of writing a “short skeleton article with almost no discussion and application and get the ideas out where people can see it and think about it.” At the same time Anderson urges Camp and Gilly to continue working on the larger project. But, then, he offers “a rather wild suggestion about the book.” The following is his statement in its entirety:

I have a rather wild suggestion about the book, and I am not at all certain if it is feasible but I should like to know what you think of it. It was originally planned that Mayr and I were to publish a joint effort. For various reasons, however, they are coming out in separate volumes. Mayr’s is in the press and I have about 100 pages of manuscript. What you have written would go fairly well with that. It is along the same line of a long chapter which I projected, but never wrote. Would you care to publish in that way provided, of course, that the Columbia Press is: a. willing to make the arrangement; b. still interested in spite of war conditions? If you are interested in some such arrangement, let me know and I will write Dobzhansky and see if anything can be done.⁸

This means that in addition to the couple of chapters Anderson had by the end of the previous summer he told Nell Horner back at the MBG as he wrapped up his time at Cold Spring Harbor, Anderson had about 100 pages by March 1942. Again, traces of that manuscript have not turned up. Mayr’s book was ready to go to press within a year of the original Jesup Lectures while Anderson lagged. But, clearly, one can now look at the 1943 Camp and Gilly paper anew for clues about Anderson’s thinking.

As for Anderson’s joint publication idea, he did raise it with the Columbia University Press and got a favorable response. Nonetheless, Anderson wrote Camp on June 23, 1942, that he had had second thoughts:

Your letter came to my desk just as I was about to write you that although I got permission from Columbia for joint authorship, I finally had come to the conclusion that your effort should be published separately. Several times this spring I have attacked the problem and every time I came to the conclusion that although what I had already written supplemented [*sic*] what you two had written very nicely indeed; the two manuscripts were composed with such different audiences in mind that they just wouldn’t fit without complete rewriting.⁹

W. H. CAMP AND BIOSYSTEMATY

Camp and C. L. Gilly published their “The Structure and Origin of Species with a discussion of intraspecific variability and related nomenclatural problems” in *Brittonia*

(Camp & Gilly, 1943). As noted above, Edgar Anderson recommended they publish a “short skeleton article with almost no discussion and application and get the ideas out where people can see it and think about it.”¹⁰ Presumably he was talking about the first ten pages, which are devoted to a preface, acknowledgments, prologue, and, to initiate the discussion of Part I, “The Species in Biosystematy,” “An Introduction to Biosystematy.” The rest of Part I is devoted to “An Analysis of the Kinds of Species,” including two kinds where apomixis (asexual reproduction) is present and 10 where it is not. The remaining 30 pages take up Part II, “On the Variability within Populations,” and Part III, “Subspecific Units and Nomenclature.” Thus, it is an ambitious paper with several, perhaps too many, aims. But it certainly received serious prepublication attention, witness the following commentators acknowledged in the text: Edgar Anderson, E. B. Babcock, Jens Clausen, R. E. Cleland, Lincoln Constance, Th. Dobzhansky, N. C. Fassett, Wm. M. Hiesey, David D. Keck, H. L. Mason, G. L. Stebbins, Jr., W. C. Steere, and Ira L. Wiggins.¹¹ This list includes a virtual “Who’s Who” of the founders of experimental taxonomy or biosystematics.

Their paper was a product of the same exciting discoveries and possibilities that drove the evolutionary synthesis proper. It was an important time to examine systematics and the structure and origin of species because, as they put it,

These most recent probings into the nature of the species (see Dobzhansky 1941 [that is, the second and, to that point, most recent edition of *Genetics and the Origin of Species*]) are yielding results which would have been as startling to the systematists of another generation as they are at times bewildering to our own. (Camp & Gilly, 1943, p. 327)

The species problem could now be subjected to more exact enquiry because

there are now at hand two things which the earlier systematists lacked: an ever-increasing mass of data on the genetic structure of populations as well as the means to analyze the mechanics of genetic variability. (Camp & Gilly, 1943, p. 327)

Through their research, they were led to correspondence with “a certain eminent cytologist” who told them he was “a little inclined to consider the advisability of giving up the term ‘species’ altogether.” They disagreed, from the viewpoint of biosystematy. Though perhaps “nothing really new” because “the systematist has long recognized that many populations are diverse—that some species are morphologically homogeneous, while others are quite variable,” biosystematy “demonstrates that specific units do exist” (Camp & Gilly, 1943, p. 324). Their fuller definition, italicized in the original, is that

biosystematy seeks (1) to delimit the natural biotic units and (2) to apply to these units a system of nomenclature adequate to the task of conveying precise information regarding their defined limits, relationships, variability, and dynamic structure. (Camp & Gilly, 1943, p. 327)

They share the systematists’ creed, born of a disciplinary experience unlike the cytologists’, that species are real units in nature. And, further, as systematists, they strive to create a nomenclature that best reflects the state of their science.

Biosystematy, though, represents an expansion of the systematist's reach. The "exploratory" stage was the necessary beginning of taxonomic research based on morphological examination of limited samples. As specimens accumulated in herbaria, information about variation and distribution within species made possible "systematic studies." But "the ultimate stage of biological systematics—biosystematy—is that wherein the group under consideration, in addition to morphological and biogeographical studies, is subjected to genetic analyses" (Camp & Gilly, 1943, p. 330).

Biosystematics is frankly synthetic. They offered their opinions unapologetically "in the form of a credo; in places we may appear to be dogmatic." Such sharply posed positions, likely discarded as the discussion unfolds, serve as much to focus a wished for more extended treatment "of the problems which mutually confront the systematist, cytologist, and geneticist. Yet we are strongly of the opinion that some conscious attempt should be made in the near future to synthesize the variant viewpoints of workers in these several disciplines" (Camp & Gilly, 1943, pp. 324–325).

From the narrower vantage point of evolutionary synthesis proper, Camp and Gilly reflect the kind of population thinking Mayr so values, insisting "The species is not necessarily a particular kind of organism; the species is a kind of population" (Camp & Gilly, 1943, p. 331).

Thus, the significant contribution of Camp and Gilly (1943) deserves attention from historians variously interested in the evolutionary synthesis, the development of evolutionary theory in the twentieth century, and plant population biology. The interest Edgar Anderson showed in it as he was working on his Jesup Lectures manuscript gives it an importance to those of us concerned with both the organizational and the scientific aspects of the evolutionary synthesis. More broadly, it reflects an important moment in evolutionary biology when advances in many disciplines including genetics, cytology, and taxonomy posed the enticing possibility of interdisciplinary interaction. Camp and Gilly were contributors to a wide-ranging discussion of which the well-recognized "architects" of the evolutionary synthesis were but the tip of the proverbial iceberg. Examining their approach and conclusions is a way of recapturing the breadth of the discussion in the synthesis period. Finally, their work is a reminder of the special insights into the process of evolution open to those working with plants and confronting their complex genetic structures and reproductive strategies.

CAMP AND GILLY (1943) ASSESSED

If, as I suggest, Camp and Gilly's article "Structure and Origin of Species" (1943) deserves the attention of historians for the reasons given above, I do not want to ignore its flaws. While acknowledged as a landmark in the forging of biosystematics, it seems by now a wholly historical document and not one returned to for ongoing insights. In my commentary, I have emphasized the general and methodological aspects of the introductory material, but those account for only 10 pages out of 61 total. In the remainder of the paper, they identify and name a dozen different types of species that result from different genetic structures. Thus, they introduce what has turned out to be their own idiosyncratic terminology, including "Allopolyploidion: a species derived by allopolyploidy; its individuals, although usually highly variable, are interfertile" (Camp & Gilly, 1943, p. 342), and "Micton: a species often of wide distribution, the result of hybridization between individuals of two or more species; all individuals are interfertile

with themselves and with the ancestral genotypes” (Camp & Gilly, 1943, p. 347). These categories and terms do not seem to have been picked up and used by their coworkers. They also include an extended nomenclatural discussion which introduces several more terms for subspecific categories (including “Phenogen,” “Forma,” “Forma apomicta,” and “Stropha” for aberrant or unusual individuals).

Criticisms along these lines were raised in the prepublication correspondence with their distinguished colleagues. Anderson, as already noted, urged a separate short theoretical introduction to initiate discussion with the longer paper with data to follow. For him, the concepts, approach, and methodology were more important than the nuances of categories and terminology. Norman Fassett, from Wisconsin, whom Mayr (Mayr & Provine, 1980, p. 138) acknowledged as a contributor to population thinking in botany along with Anderson, wrote Camp to say, “The paper as a whole of tremendous value to the taxonomist. A lot of junk in some places; reducing 50% would raise value 500%.”¹² G. L. Stebbins agreed “that it is a bit long and wordy” and urged Camp and Gilly to remember the students “not being familiar with the various arguments of other botanists, will find these lengthy arguments of yours rather tedious, and will be satisfied with much less.” Better to write to them “because we cannot hope to convert the old reactionaries.”¹³ E. B. Babcock agreed that it had “too great length and too many minor details which tend to frustrate achieving the main goal.”¹⁴ Camp, though, summarized the discussion on the length of the paper in a letter to Stebbins: “With some wanting it shorter and some longer maybe we are about right!!!”¹⁵

Camp also heard his colleagues’ doubts about the usefulness of their new terminology. Fassett observed, “You show a Clementsian faculty for burdening obvious and well-known facts with occult and unfamiliar names. You might as well explain, and name all the steps, in walking from the El station to the Gardens.”¹⁶ More gently, Stebbins was “inclined to feel that a modification of your nomenclature would help matters a good deal. Greek substantives look very threatening to young students and sometimes leave a rather bad taste in the mouths of older people.”¹⁷

By distributing their draft to those working along similar lines, Camp initiated a fruitful exchange that advanced biosystematics generally. Camp told Stebbins, “Both Anderson and Babcock have tipped us off to papers (their own and others) which should be mentioned. We hope you will do the same.”¹⁸ Both David Keck and Jens Clausen of the Carnegie Institution of Washington Division of Plant Biology based at Stanford wrote lengthy letters (14 and 12 pages, respectively) to Camp drawing on their research into what they called “experimental taxonomy.” Keck pointed out “that you have disregarded a now considerable literature on this very subject which covers many points that you discuss as though they had never been expressed before.”¹⁹

This exchange of information, references, and citation served to sharpen the thinking of all those working along biosystematic lines, whether they were in New York, the Bay Area (Stebbins, Babcock, Clausen, Keck, and their colleague William Hiesey), or the Midwest (Anderson and Fassett).

In the Bay Area there was a group that actually called themselves the Biosystematists or the Biosystematic Group (Hagen, 1983, 1984; Smocovitis, 1992, 1996). Both Keck and Lincoln Constance from the University of California Herbarium called this ongoing, multi-institutional seminar to Camp’s attention. Keck continued his general comments by noting

that your conclusions, so considerably theoretical, do not satisfy us experimentalists who are amassing and evaluating the sort of cytogenetic and other data that must be the kinds of keystones used to build any classification that will fit our needs as biosystematists. We have a San Francisco Bay Region seminar group of some 25 to 30 botanists and zoologists who meet regularly to discuss problems of evolution and distribution known as The Biosystematics.²⁰

Constance noted, “Out here, largely through our organization—the Biosystematists—we have been discussing & considering the impact of genetics and other fields on Systematics for five or six years. Thus, even Dobshansky’s [*sic*] book doesn’t blast us completely out of our wits.”²¹

THE ROOTS OF BIOSYSTEMATICS

As Constance’s observation indicates, those drawn to biosystematics were synthesizing both experimental, laboratory-based findings from genetics and cytology with field studies in ecology and evolution in this key period. Such workers at once anticipated, contributed to, and were a receptive audience for the evolutionary synthesis.

The development of experimental taxonomy or biosystematics²² was a line of enquiry where Gregor Mendel’s ideas on genetics could be incorporated into the study of evolution and its processes. As Joel Hagen has observed,

In addition, among taxonomists there was considerable interest in methods and ideas from other disciplines, and a number of important biologists took an active interest in taxonomic problems. Indeed, between 1920 and 1950 there were several notable examples of cooperative research involving taxonomists, ecologists, geneticists, and cytologists. To be sure, such cooperative ventures did not involve a majority of workers in any of these fields. But such activity was more prevalent than has been supposed and was certainly not limited only to the major figures in the Modern Synthesis. (Hagen, 1984, p. 250)

Fredrick Clements is one early contributor to this approach. As an ecologist he criticized harshly orthodox taxonomy for not going beyond descriptive botany to incorporate phylogenetic relationships and thus giving rise to a wide range of interpretation of what constituted a race, variety, or even species. It needed to be transformed “from a field overgrown with personal opinions to one in which scientific proof is supreme” via populational studies of plants over their entire ranges as well as transplant experiments (Hall & Clements, 1923, p. 3).

By growing cuttings from the same plant ideally in experimental gardens under a variety of environmental situations (Clements used plots at various altitudes on Pike’s Peak while his collaborator Harvey Monroe Hall had a similar arrangement in California), one could “determine the effect of changed and measured habitats in causing adaptation and variation and in producing new forms” (Clements & Hall, 1919, pp. 334–335). Indeed, Clements claimed in a Lamarckian fashion that he had been able to transform one species to another by moving it to a new environment.

Göte Turesson used Clements’s and Hall’s transplant experiment model in reverse, as it were. He brought plants from various habitats to a controlled garden plot in

hopes that accidental environmental modifications of the phenotype would disappear, revealing the underlying genotype at the core.

Hall, in addition to working with Clements, collaborated with E. B. Babcock on tarweeds (*Hemizonia*) in 1924 (Babcock & Hall, 1924). Hall also launched Babcock on his study of the Genus *Crepis*. When it appeared in 1947, Anderson, in his review “The Definitive Hawks Beard,” termed it a “masterpiece” and marveled at both the breadth of the scholarship and the web of institutional support Babcock maintained over nearly three decades (Anderson, 1948).

G. Ledyard Stebbins, who himself participated in the project, in his biographical memoir of Babcock termed the study “to this date the foremost attempt to explain the evolution of a genus of plants primarily on a genetic basis, while considering at the same time all other possible avenues of approach” (Stebbins, 1968).

Hall also began assembling the Carnegie Institution of Washington team, which Jens Clausen led after Hall’s untimely death in 1932. Early in their project, Clausen, David Keck, and William Hiesey set explicitly evolutionary aims:

With taxonomic, cytologic, and genetic data at hand, it is often possible to form hypotheses as to how certain groups evolved from others. The attempt is made to repeat Nature’s course of evolution by laboratory manipulation. (Clausen, Keck, & Hiesey, 1932)

They also used transplant experiments in a number of studies of California plants that refuted Clements’s Lamarckian claims of species transformation by changing the environment, while exploring such topics as the evolution of genetic barriers and the genetic structure of ecological races from the 1930s on.

CONCLUSION

It is this tendency of evolutionary plant scientists working across several disciplines to resolve evolutionary questions that Anderson’s work contributed to and complemented. For him, it was frankly synthetic work, whatever judgment we ultimately make about its relation to the evolutionary synthesis proper. Anderson was drawn to the idea of biosystematics as a disciplinary “no-man’s-land.” He reviewed Stanley A. Cain’s *Foundations of Plant Geography* in just such terms. Books such as this one, Anderson argued, were necessary to make the findings of several fields accessible to other interested workers:

A concept which is becoming increasingly prevalent in genetics is the notion that natural selection operates not upon the individual species as such but upon the entire biological spectrum of any particular habitat. More than one able geneticist has started out to do exact quantitative field work on micro-evolution only to find that before the investigation could get down to fundamentals exact cyto-genetic techniques would have to be accompanied by equally precise ecological analysis. There is therefore an urgent need for books which make cytogenetics understandable (and palatable) to ecologists and plant geographers, and *vice versa*. (Anderson, 1944, p. 349)

He had used the same phrase in a note scribbled on Camp and Gilly’s draft at the point where they introduce the term “biosystematy,” “which was the point of the letters I wrote you a year ago about the no-man’s land (biosystematy) between Genetics and

Hayloft Taxonomy!”²³ He had little patience for bureaucratic obstacles. In a pointedly titled chapter, “Budgets vs. Scholarship,” in his *Plants, Man and Life*, he observed,

Problems which fall straight across departmental and divisional lines run into administrative red tape. A whole series of coherent, fundamental questions are neglected because they do not fall clearly within the domain of a single discipline. . . . Knowledge is all of one piece but universities (by tradition and for budgetary reasons) are divided into departments. (Anderson, 1952, pp. 108, 110)

Such unconventionality made Anderson a polarizing figure among colleagues. G. Ledyard Stebbins remembered his friend this way:

The personality of Edgar Anderson, combining a capacity for precise, careful observation and logical deduction with flamboyant showmanship and a penchant for intemperate attacks on those whom he regarded as misguided or stupid, was bound to make implacable enemies as well as devoted friends. (Stebbins, 1979, p. 24)

Interestingly, W. H. Camp was eulogized similarly in an obituary in *Taxon*:

Camp was iconoclastic and unsparing of strictures on his colleagues in taxonomy. Many botanists regarded him as something of a clown, a “bad boy,” an irresponsible egoist. He was none of these, in spite of much colorful and often exaggerated talk. (Rickett, 1963)

The prospect of a collaboration between such creative and occasionally acerbic plant scientists at such a key point in evolutionary studies as the early 1940s is exciting to consider on its own terms. Insofar as Anderson’s overture to Camp adds clues to the fate of his uncompleted Jesup Lectures manuscript, it is of wider importance.

Yet, ultimately, this episode perhaps best serves as a reminder that several botanists were synthesizing Mendelian genetics, systematics, and natural history by way of enriching evolutionary theory in the first decades of the twentieth century. This ought not be surprising, from Mendel himself through his rediscoverers’ research in heredity (and subsequently genetics) was frequently with conducted with plants as the organisms of choice. Lots of evolution over a very long period of time has occurred in plants. Yet, in the aftermath of the evolutionary synthesis our evolutionary models are too rarely botanical and the impression persists that botany came late to the synthesis project.

G. Ledyard Stebbins is justly celebrated for his monumental (1950) *Variation and Evolution in Plants*, based on his own 1946 Jesup Lectures. On that basis, he is often perceived as *the* synthesis botanist. For example, he participated in the first of the two conferences Ernst Mayr organized in 1974 on the evolutionary synthesis that led to the Mayr-Provine volume in 1980. Stebbins’s contribution to that book, “Botany and the Synthetic Theory of Evolution” (Stebbins, 1980), reflects the consensus forged through Mayr’s project. There, Stebbins observes that botanists in general were hampered by the lack of appreciation of natural history by their taxonomy professors—Willis Linn Jepson and then Lincoln Constance at the University of California, Berkeley, and Arthur Cronquist at the New York Botanical Garden among them. “Although they [plant taxonomists] went into the field to collect specimens they paid little attention to plants as living organisms,” he observed (Stebbins, 1980, p. 150). Further, in botany

“the only people who thought above the species level were the morphologists and the anatomists,” and such workers as Agnes Arber and Liberty Hyde Bailey of Cornell University viewed such Darwinian concepts as adaptation and selection as teleological (Stebbins, 1980, p. 150).

For this audience of historians and synthesis veterans, Stebbins rehearsed the history of biosystematics, noting the roles of such key figures as Gote Turesson, Frederick Clements, Harvey Monroe Hall, and Jens Clausen, and his colleagues David Keck and William Hiesey. The framework is Mayr’s. Turesson, for example, is criticized for being “mistaken about the pattern of racial variation within the species. As Mayr has commented, Turesson was definitely a typologist” (Stebbins, 1980, p. 141). Thus, he was unable to utilize the Biological Species Concept which, with population thinking, is among the key linchpins of the evolutionary synthesis Mayr identified—“although Turesson knew about reproductive isolation barriers, he did very little to explore them” (Stebbins, 1980, pp. 141–142).

But, even within this historiography, Stebbins begins by asserting that

Botany made three kinds of contributions to the synthetic theory: first, its discovery of the facts that were necessary before the synthesis could be built; second, plant science’s actual syntheses; and third, the reception of these syntheses by both other plant scientists and the biological community in general. (Stebbins, 1980, p. 139)

Botanists contributed many of the key genetic discoveries on which the evolutionary synthesis was based. But, further, Stebbins intimates that plant scientists pursued their own syntheses such as biosystematics or experimental taxonomy independent of the broader biological community which incorporated some, but not all, of these insights into the evolutionary synthesis.

Just a few years later to an audience of younger colleagues in plant population biology at a 1977 conference at Cornell University, Stebbins dealt with Turesson and this whole biosystematic history differently. There, Stebbins was free to celebrate Turesson for conducting influential “pioneer experiments [that] developed methods to answer” (Stebbins, 1979, p. 26) questions about variation within species. He also offered a different view of the Biological Species Concept, agreeing with “many botanists” who

have regarded the acknowledged prevalence of natural hybridization between distinct populations of plants as a reason for rejecting the biological species concept. Undoubtedly, the claim that some zoologists have made for this concept, that it removes subjectivity and arbitrariness from the delimitation of species, is not valid for plants. (Stebbins, 1979, pp. 24–25)

This hardly means that Stebbins is left with relying solely on morphological data to define species. He is clear that such definitions are “useless.” In fact, “species definitions based at least partly upon reproductive isolation under natural conditions are of great value for understanding critical steps of the evolutionary process” (Stebbins, 1979, p. 25). But it is worth noting first that Stebbins here acknowledges multiple species definitions and, secondly, that they need be only partly based on the reproductive isolation that is the *sine qua non* of the Biological Species Concept.

From the beginning of his essay, Stebbins is clearly outside the framework of Mayr's historiography. His very title is "Fifty Years of Plant Evolution" and since he presented these ideas in 1977 and then published them in 1979, he tracked a very different period. While this might primarily be explained by the fact that he was chronicling the course of plant evolution over his own career, which began in the 1920s, nonetheless he comments about population genetics that "its marriage with ecology which produced the modern, dynamic approach to the processes of evolution was not consummated until the 1960s" (Stebbins, 1979, p. 18). Though in 1963, Mayr did acknowledge that "Each of the kingdoms has its own evolutionary peculiarities and these must be worked out separately before a balanced synthesis can be attempted" (Mayr, 1963, p. v), he saw the evolutionary synthesis as consolidated by the January 2–4, 1947, conference at Princeton called by the Committee on Common Problems of Genetics, Paleontology, and Systematics (Jepsen, Mayr, & Simpson, 1949), and the launching of the journal *Evolution* by the Society for the Study of Evolution (Cain, 1993, 1994, 2000b, Smocovitis, 1992, 1994a, 1994b, 1996). Stebbins, at least to a group of fellow botanists, offered a contrary view.

Clearly, though, something very important happened in evolutionary studies in the second quarter of the twentieth century. The work of R. A. Fisher, Sewall Wright, J. B. S. Haldane, Theodosius Dobzhansky, Ernst Mayr, George Gaylord Simpson, G. Ledyard Stebbins, and many others will warrant the attention of generations of historians of biology. Yet, in looking at the contributions of Edgar Anderson, W. H. Camp, and other biosystematists and considering plant scientists' own version of their history as exemplified by Stebbins's 1979 essay, the crisp outlines of the evolutionary synthesis may blur. We may come to view the evolutionary synthesis the way Steven Shapin views the Scientific Revolution—there is no such thing, but, please, let there be many books, articles, and conferences on it (Shapin, 1996, p. 1). We need both to shine beacons at it and probe the shadows our beacons cast.

NOTES

1. See Anderson (1956a and 1956b). When Anderson visited Princeton's math department at the invitation of John Tukey in early 1957, Fisher came to the campus to meet with him and Tukey.
2. Anderson (1936b, 1937), Anderson and Hubricht (1938), Anderson and Woodson (1935), Sax and Anderson (1933, 1934a, 1934b, 1936).
3. Mayr to Kleinman, May 16, 1995. In author's possession.
4. Mayr to Kleinman, May 16, 1995. In author's possession.
5. "Anderson" interview for *Making of a Scientist*. Anne Roe Papers, American Philosophical Society.
6. Anderson to Horner, late summer 1941, Anderson Papers, Archives of the Missouri Botanical Garden. RG 3/2/4; Series 3; Edgar Anderson Papers: Correspondence: January 17, 1931–May 9, 1946; Box 10 of 36; Folder 14.
7. Camp and Gilly (1943) For the section on "Allopolyploidism," see pp. 342–348.
8. Anderson to Camp, March 20, 1942. W. H. Camp papers, New York Botanical Garden Archives (hereafter, Camp Papers).
9. Anderson to Camp, June 23, 1942, Camp Papers.
10. Anderson to Camp, March 20, 1942, Camp Papers.
11. E. B. Babcock (1877–1954) University of California-Berkeley geneticist-taxonomist. Jens Clausen (1891–1969) Carnegie Institution of Washington experimental taxonomist. R. E.

- Cleland (1892–1971) University of California-Berkeley geneticist. Lincoln Constance (1909–2001) University of California-Berkeley botanist. N. C. Fassett (1900–1954) University of Wisconsin taxonomist. William Hiesey (1903–1998) Carnegie Institution of Washington experimental taxonomist. David Keck (1903–1995) Carnegie Institution of Washington experimental taxonomist. H. L. Mason (1896–1994) University of California-Berkeley taxonomist. W. C. Steere (1907–1989) New York Botanical Garden bryologist. Ira L. Wiggins (1899–1997) Stanford University botanist.
12. Fassett to Camp, undated, Camp Papers.
 13. Stebbins to Camp, March 14, 1942, Camp Papers.
 14. Babcock to Camp, March 13, 1942, Camp Papers.
 15. Camp to Stebbins, March 23, 1942, Camp Papers.
 16. Fassett to Camp, undated, p. 3. Camp Papers.
 17. Stebbins to Camp, March 14, 1942. Camp Papers.
 18. Camp to Stebbins, March 23, 1942, Camp Papers.
 19. Keck to Camp, March 23, 1942, Camp Papers.
 20. Keck to Camp, March 23, 1942, Camp Papers.
 21. Constance to Camp, March 15, 1942. Camp Papers.
 22. For fuller discussions, see Chambers (1995) and Hagen (1983, 1984). I also have benefited from discussions on these matters with Alan Whittemore of the United States National Arboretum and with J. Chris Pires on the work of Jens Clausen, David Keck, and William Hiesey, including his paper at the 2000 History of Science Society meetings in Vancouver, British Columbia.
 23. “Camp, W. H., Systematics & Species by W. H. Camp & C. L. Gilly Ms. Copy sent to E. A. Anderson, 1942,” Camp Papers.

REFERENCES

- Anderson, E. (1924). Studies on self-sterility VI. The genetic basis of cross-sterility in *Nicotiana*. *Genetics*, 9, 13–40.
- Anderson, E. (1928). The problem of species in the northern blue flags, *Iris versicolor* L. and *Iris virginica* L. *Annals of the Missouri Botanical Garden*, 15, 241–332.
- Anderson, E. (1936a). The species problem in *Iris*. *Annals of the Missouri Botanical Garden*, 23, 457–509.
- Anderson, E. (1936b). Hybridization in American *Tradescantias*. *Annals of the Missouri Botanical Garden*, 23, 511–523.
- Anderson, E. (1937). Hybridization in *Tradescantia*. *Genetics*, 22, 183.
- Anderson, E. (1940). Edward Murray East (1879–1938). *Proceedings of the American Academy of Arts and Sciences*, 74, 117–118.
- Anderson, E. (1944). [Review of the book *Plant geography: The biosystemic no-man's land*]. *Journal of Heredity*, 35, 349–351.
- Anderson, E. (1948). The definitive Hawks-Beard [Review of the book *The Genus Crepis* by Ernest Brown Babcock.]. *Journal of Heredity*, 39, 243–244.
- Anderson, E. (1949). *Introgressive hybridization*. New York: John Wiley and Sons.
- Anderson, E. (1952). *Plants, man and life*. Boston: Little, Brown.
- Anderson, E. (1956a). Missouri vegetation and an English mathematician. *Missouri Botanical Garden Bulletin*, 44, 12–14.
- Anderson, E. (1956b). Why botanists visit math departments. *Missouri Botanical Garden Bulletin*, 44, 148–151.
- Anderson, E. (1956c). [Review of the book *Evolution, genetics, and man*]. *Bulletin of the Torrey Botanical Club*, 83, 441.

- Anderson, E. (1968). What we do not know about *Zea Mays*. *Transactions of the Kansas Academy of Sciences*, 71, 373–378.
- Anderson, E. (n.d.). *Kinsey as I knew him*. Unpublished manuscript (Anderson folder), Kinsey Institute archives (Bloomington, IN).
- Anderson, E., & Hubricht, L. (1938). Hybridization in *Tradescantia* III. The evidence for introgressive hybridization. *American Journal of Botany*, 25, 396–402.
- Anderson, E., & Palmer, E. J. (1935). *Uvularia perfoliata* in Louisiana. *Rhodora*, 37, 58–59.
- Anderson, E., & Whittaker, T. W. (1934). Speciation in *Uvularia*. *Journal of the Arnold Arboretum*, 15, 28–42.
- Anderson, E., & Woodson, R. E. (1935). The species of *Tradescantia* indigenous to the United States. *Contributions of the Arnold Arboretum*, 9, 1–132.
- Babcock, E. B., & Hall, H. M. (1924). *Hemizonia congesta*. A genetic, ecologic, and taxonomic study of the hay-field tarweeds. *University of California Publications in Botany*, 13, 12–100.
- Cain, J. (1993). Common problems and cooperative solutions: Organizational activity in evolutionary studies, 1936–1947. *Isis*, 84, 1–25.
- Cain, J. (1994). Ernst Mayr as community architect: Launching the Society for the Study of Evolution and the journal *Evolution*. *Biology and Philosophy*, 9, 387–427.
- Cain, J. (2000a). Towards a “greater degree of integration”: The Society for the Study of Speciation, 1939–1941. *British Journal for the History of Science*, 33, 85–108.
- Cain, J. (2000b). For the “promotion” and “integration” of various fields: First years of *Evolution*, 1947–1949. *Archives of Natural History*, 27, 231–259.
- Cain, J. (2001). The Columbia Biological Series, 1984–1974: A bibliographic note. *Archives of Natural History*, 28, 353–366.
- Cain, J. (2002a). Co-opting colleagues: Appropriating Dobzhansky’s 1936 lectures at Columbia. *Journal of the History of Biology*, 35, 207–219.
- Cain, J. (2002b). Epistemic and community transition in American evolutionary studies: The “Committee on Common Problems of Genetics, Paleontology, and Systematics” (1942–1949). *Studies in History and Philosophy of Biological and Biomedical Sciences*, 33, 283–313.
- Camp, W., & Gilly, C. L. (1943). Structure and origin of species. *Brittonia*, 4, 324–385.
- Chambers, K. L. (1995). The contributions of Göte Turesson to plant taxonomy. In A. R. Kukeberg, R. B. Walker, & A. Leviton (Eds.), *Genecology and ecogeographic races: Papers in the biological sciences presented at the 73rd Annual Meeting of the Pacific Division AAAS on the occasion of the 100th anniversary of the birth of Göte Turesson* (pp. 37–55). San Francisco: Pacific Division AAAS.
- Clausen, J., Keck, D., & Hiesey, W. (1932). Experimental taxonomy. *Carnegie Institution of Washington Yearbook*, 31, 201–205.
- Clements, F. E., & Hall, H. M. (1919). Experimental taxonomy. *Carnegie Institution of Washington Yearbook*, 18, 334–335.
- Dobzhansky, T. (1937). *Genetics and the origin of species*. New York: Columbia University Press.
- Fisher, R. A. (1936). The use of multiple measurements in taxonomic problems. *Annals of Eugenics*, 7, 179–188.
- Gould, S. J. (1983). The hardening of the modern synthesis. In M. Grene (Ed.), *Dimensions of Darwinism: Themes and counter-themes in twentieth-century evolutionary theory* (pp. 71–93). Cambridge: Cambridge University Press.

- Hagen, J. B. (1983). The development of experimental methods in plant taxonomy, 1920–1950. *Taxon*, 32, 406–416.
- Hagen, J. B. (1984). Experimentalists and naturalists in twentieth-century botany: Experimental taxonomy, 1920–1950. *Journal of the History of Biology*, 17, 249–270.
- Hall, H. M., & Clements, F. E. (1923). *The phylogenetic method in taxonomy: The North American species of Artemisia, Chrysothamnia, and Atriplex*. Carnegie Institution of Washington, 326, iv, 355.
- Jepsen, G. L., Mayr, E., & Simpson, G. G. (Eds.). (1949). *Genetics, paleontology, and evolution*. Princeton, NJ: Princeton University Press.
- Kohler, R. E. (2002). *Landscapes and labscapes: Exploring the lab-field border in biology*. Chicago: University of Chicago Press.
- Kleinman, (1999). His own synthesis: Corn, Edgar Anderson, and evolutionary theory in the 1940s. *Journal of the History of Biology*, 32, 293–320.
- Mayr, E. (1963). *Animal species and evolution*. Cambridge, MA: Belknap Press of Harvard University Press.
- Mayr, E. (1999). *Systematics and the origin of species: From the viewpoint of a zoologist*. Cambridge, MA: Harvard University Press.
- Mayr, E., & Provine, W. B. (Eds.). (1980). *The evolutionary synthesis: Perspectives on the unification of biology*. Cambridge, MA: Harvard University Press.
- Provine, W. B. (2001). *Origins of theoretical population genetics*. Chicago: University of Chicago Press.
- Rickett, H. W. (1963). Wendell Holmes Camp, 1905–1963. *Taxon*, 12, 276–279.
- Roe, A. (1953). *The making of a scientist*. New York: Dodd and Mead.
- Sax, K., & Anderson, E. (1933). Segmental interchange in chromosomes of *Tradescantia*. *Genetics*, 18, 53–67.
- Sax, K., & Anderson, E. (1934a). Interlocking bivalent chromosomes in *Tradescantia*. *Genetics*, 19, 157–166.
- Sax, K., & Anderson, E. (1934b). A cytological analysis of self-sterility in *Tradescantia*. *Botanical Gazette*, 95, 609–621.
- Sax, K., & Anderson, E. (1936). A cytological monograph of the American species of *Tradescantia*. *Botanical Gazette*, 97, 433–476.
- Shapin, S. (1996). *The scientific revolution*. Chicago: University of Chicago Press.
- Smocovitis, V. B. (1992). Unifying biology: The evolutionary synthesis and evolutionary biology. *Journal of the History of Biology*, 25, 1–65.
- Smocovitis, V. B. (1994a). Organizing evolution: Founding the Society for the Study of Evolution (1939–1950). *Journal of the History of Biology*, 27, 241–309.
- Smocovitis, V. B. (1994b). Disciplining evolutionary biology: Ernst Mayr and the founding of the Society for the Study of Evolution and *Evolution* (1939–1950). *Evolution*, 48, 1–8.
- Smocovitis, V. B. (1996). *Unifying biology: The evolutionary synthesis and evolutionary biology*. Princeton, NJ: Princeton University Press.
- Stebbins, G. L. (1950). *Variation and evolution in plants*. New York: Columbia University Press.
- Stebbins, G. L. (1968). Ernest Brown Babcock, *Biographical memoirs of the National Academy of Science*, 32, 50–66.
- Stebbins, G. L. (1979). Fifty years of plant evolution. In O. T. Solbrig, S. Jain, G. B. Johnson, & P. H. Raven (Eds.), *Topics in plant population biology* (pp. 18–41). New York: Columbia University Press.

Stebbins, G. L. (1980). Botany and the synthetic theory of evolution. In E. Mayr & W. B. Provine (Eds.), *The evolutionary synthesis: Perspectives on the unification of biology* (pp. 139–152). Cambridge, MA: Harvard University Press.