VASSILIKI BETTY SMOCOVITIS*

The "Plant *Drosophila*": E. B. Babcock, the Genus *Crepis*, and the Evolution of a Genetics Research Program at Berkeley, 1915–1947

The student of genetics must be ready to resort to the use of any living organism that gives promise of revealing the natural laws upon which the future science of breeding will be grounded.
E. B. Babcock, 1913[1]

The Crepis investigations carried on by the Babcock group are the American evolutionary investigations that seem to have attracted the largest attention outside of America next to the Drosophila investigations. One reason for this is their wider systematical aspect.
Jens Clausen, 1934[2]

*Departments of Zoology and History, Affiliate in Botany, University of Florida, Bartram Hall, Gainesville, FL 32611; bsmocovi@zoo.ufl.edu, bsmocovi@history.ufl.edu.

The following abbreviations are used: APS, American Philosophical Society Library, Philadelphia, PA; CAS, California Academy of Sciences, San Francisco, CA; CIW, Carnegie Institution of Washington; CP, Carnegie Papers, Missouri Botanical Garden Archives, St. Louis, MO; EBB, Ernest Brown Babcock Papers, TBL; *JHB*, *Journal of the History of Biology*; JAJ, James Angus Jenkins Papers, TBL; RG, Rockefeller Foundation Archives, Sleepy Hollow, NY, http://www.rockarch.org/collections/rf/; TBL, The Bancroft Library, University of California, Berkeley; UC, University of California; UCGD, University of California, Berkeley, Genetics Department, APS. Interviews with G. Ledyard Stebbins are transcribed and in the author's possession.

1. "Division of Genetics: Report to the Director of the Experiment Station, 11 June 1913," EBB, Folder The Division of Genetics of the Department of Agriculture. See also the mission statement of the division in document titled "Department of Genetics," 7 Apr 1956, JAJ, Box 2, Folder History of Department.

2. Jens Clausen, "Memorandum re Babcock's Proposed New Program on the Crepidinae," 24 Sep 1934, CP, Folder Correspondence, Dr. E. B. Babcock Through September 11, 1946.

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ABSTRACT

This paper explores the research and administrative efforts of Ernest Brown Babcock, head of the Division of Genetics in the College of Agriculture at the University of California, Berkeley, the first academic unit so named in the United States. It explores the rationale for his choice of "model organism," the development—and transformation—of his ambitious genetics research program centering on the weedy plant genus named *Crepis* (commonly known as the hawkbeard), along with examining in detail the historical development of the understanding of genetic mechanisms of evolutionary change in plants leading to the period of the evolutionary synthesis. Chosen initially as the plant counterpart of Thomas Hunt Morgan's *Drosophila melanogaster,* the genus *Crepis* instead came to serve as the counterpart of Theodosius Dobzhansky's *Drosophila pseudoobscura*, leading the way in plant evolutionary genetics, and eventually providing the first comprehensive systematic treatise of any genus that was part of the movement known as biosystematics, or the "new" systematics. The paper also suggests a historical rethinking of the application of the terms model organism, research program, and experimental system in the history of biology.

KEY WORDS: Berkeley, *Crepis*, E. B. Babcock, G. L. Stebbins, evolutionary synthesis, plant genetics and evolution, polyploid complex, biosystematics, model organism

INTRODUCTION

In 1912 a new building was added to the skyline of the University of California at Berkeley. Named Agriculture Hall, the new building's dedication was met with much fanfare, celebration, and commemoration that included the installation of a new Dean of the College of Agriculture (and Director of the Agricultural Experiment Station), Thomas Forsyth Hunt, and a specially designed bronze bust of his visionary predecessor, Eugene Woldemar Hilgard.[3] The new building was important: it embodied all the aspirations of California agriculturalists as the state entered the second decade of the twentieth century. The hope was that the "New" College of Agriculture would fulfill the agricultural mission of the state through the kind of teaching and research that would also impart moral instruction and discipline, and at the same time control the

3. Hilgard had a second building named after him in 1917 with another special dedication ceremony. Accompanying it were exhibits from California nurseries, growers, and horticulturalists. See "Hundreds of People Visited Genetics Exhibit," 1917, JAJ, Box 1, Folder Roy Elwood Clausen.

"invading hordes" of immigrants whose foreign lifestyles and values threatened to upset the moral economy of the state.[4]

As part of the new organization of the college, the Division of Genetics was created, the first such unit with that name in the nation.[5] The individual chosen to lead the division was Ernest Brown Babcock, known for his work in plant breeding, but also for his experience and dedication to agricultural instruction. From 1913 through 1947, Babcock recruited faculty, students, and staff from all over the world to Berkeley, and supervised a series of administrative reforms that would build one of the most influential genetics units in the world. He was also at the helm of one of the most ambitious genetics research programs at the time, creating an entire school of evolutionary genetics, which at its peak from the mid-1920s to the late 1930s employed over a dozen research scientists, technicians, and students, and resulted in a series of important publications that transformed the understanding of genetic evolutionary processes in the plant world. Ironically, however, while Babcock's directive was to build and enhance the agricultural mission of his division, his own celebrated research program centered on the genetics of the genus *Crepis,* a lowly weed, with no discernible value to agriculture. Originally designed to corroborate the insights emerging from Thomas Hunt Morgan's celebrated researches on *Drosophila melanogaster*, Babcock's research program took a novel direction that made plant evolution the centerpiece of genetic research efforts at the University of California at Berkeley, and in the Bay Area as a whole.

This paper aims to explore the development—indeed, the evolution—of Babcock's research program, his rationale and choice of living organism for genetical study, and the transition from plant breeding to genetics, to evolutionary

4. The rationale and mission of the new College of Agriculture is laid out in the University of California, College of Agriculture, *Record of the Dedication of the New College of Agriculture and the Installation of Dean Thomas Forsyth Hunt, 1912* (Berkeley: University of California Press, 1912); copy located at TBL. Fear of immigrant hordes was explicitly noted in the record. For more on the historical backdrop to the College of Agriculture, and the history of the land-grant university and agriculture in California, see Ann Foley Scheuring, Chester O. McCorkle, and James Lyons, *Science and Service: A History of the Land-Grant University and Agriculture in California* (Oakland, CA: Agriculture and Natural Resource Publications, University of California, 1995). See also V. A. Stadtman and the Centennial Publications Staff, ed., *The Centennial Record of the University of California* (Berkeley: University of California, 1968).

5. For the political backdrop to this founding, as well as to the founding of comparable units at Cornell University and at the University of Wisconsin, see Barbara Ann Kimmelman, "A Progressive Era Discipline: Genetics at American Agricultural Colleges and Experiment Stations, 1900–1920" (PhD dissertation, University of Pennsylvania, 1987).

genetics, and then to plant evolutionary biology.[6] Its intent is to introduce historians of science to an influential but largely forgotten scientific and administrative leader, an ambitious and influential genetics research program located at the University of California during a critical interval of its history, and an underappreciated "model" organism chosen to serve as the "plant *Drosophila.*"[7]

6. By "research program," I mean a clearly defined set of questions, established methods, and designated sources, on a well-defined research subject that is pursued methodically and with rigor over a sustained period of time. The literature on related research schools, "invisible colleges," or other social organizations in the history of science is vast. For the most recent example exploring the notion of research program in the biomedical sciences see Hans-Jörg Rheinberger, *Toward a History of Epistemic Things* (Palo Alto, CA: Stanford University Press, 1997).

7. The phrase "plant *Drosophila*" was used repeatedly by George Ledyard Stebbins as was "plant counterpart" of *Drosophila*. Interview by author, Jan 1987; and see George Ledyard Stebbins, "Ernest Brown Babcock," *Dictionary of Scientific Biography, Supplement II*, ed. Frederic L. Holmes (New York: Charles Scribner's Sons, 1990), 42–43. For more on Morgan, his research program, and *Drosophila*, see Garland E. Allen, "The Introduction of *Drosophila* into the Study of Heredity and Evolution, 1900–1910," *Isis* 66 (1975): 322–33; Garland E. Allen, *Thomas Hunt Morgan: The Man and His Science* (Princeton: Princeton University Press, 1978). On the rival maize genetics programs see Nathan Comfort, *The Tangled Field* (Cambridge, MA: Harvard University Press, 2001); Lee B. Kass, Chris Bonneuil, and Ed Coe, "Cornfests, Cornfabs and Cooperation: The Origins and Beginnings of the Maize Genetics Cooperation News Letter," *Genetics* 169 (2005): 1787–97; Lee B. Kass and Christophe Bonneuil, "Mapping and Seeing: Barbara McClintock and the Linking of Genetics and Cytology in Maize Genetics, 1928–1935," in *Classical Genetic Research and Its Legacy: The Mapping Cultures of 20th-Century Genetics,* ed. Hans-Jörg Rheinberger and Jean-Paul Gaudilliere (London: Routledge, 2005), 91–118. For the origins of population and evolutionary genetics see William B. Provine, *Origins of Theoretical Population Genetics* (Chicago: University of Chicago Press, 1971); William B. Provine, "Origins of the Genetics of Natural Population Series," in *Dobzhansky's Genetics of Natural Populations I–XLIII,* ed. R. C. Lewontin, John A. Moore, William B. Provine, and Bruce Wallace (New York: Columbia University Press, 1981), 1–83; William B. Provine, *Sewall Wright and Evolutionary Biology* (Chicago: University of Chicago Press, 1986). For a comparative dimension see Jonathan Harwood, *Styles of Scientific Thought: The German Genetics Community 1900–1933* (Chicago: University of Chicago Press, 1993). For literature on model organisms see Barbara Kimmelman, "Organisms and Interests: R. A. Emerson's Claims for the Unique Contributions of Agricultural Genetics," in *The Right Tools for the Job: At Work in Twentieth-Century Life Sciences*, ed. Adele Clarke and Joan Fujimura (Princeton: Princeton University Press, 1992), 198–322; Robert E. Kohler, *Lords of the Fly: Drosophila and the Experimental Life* (Chicago: University of Chicago Press, 1994); Angela N. H. Creager, *The Life of a Virus: TMV as an Experimental Model, 1930–1965* (Chicago: University of Chicago Press, 2001); Karen A. Rader, *Making Mice: Standardizing Animals for American Biomedical Research, 1900–1955* (Princeton: Princeton University Press, 2004); Rachel Allyson Ankeny, "The Conqueror Worm: An Historical and Philosophical Examination of the Use of the Nematode *Caenoahrbditis elegans* as a Model Organism" (PhD dissertation, University of Pittsburgh, 1997). For a recent general history of biology from the viewpoint of an experimental or model organism see Jim Endersby, *A Guinea Pig's History of Biology* (London: William Heinemann, 2007); and see also Angela Creager, Elizabeth Lunbeck, and M. Norton Wise, eds., *Science without Laws: Model Systems, Cases, Exemplary Narratives* (Durham, NC: Duke University Press, 2007).

Though not its original goal, by the end this research program produced a number of insights that resolved long-standing issues in plant genetics and evolution, helping to consolidate the growing consensus on the evolutionary synthesis with examples from the plant world; it also inspired international research initiatives and ensured the continuation of Babcock's research program at Berkeley and in the work of protégés, such as G. Ledyard Stebbins at the University of California at Davis. Historical study of the genus *Crepis*, E. B. Babcock, and his research program at Berkeley may also suggest a rethinking of the historical application of terms such as model organism, research program, and experimental system.

ERNEST BROWN BABCOCK (1887–1954): EDUCATION AND EARLY CAREER

As much a keen administrator, organizer, and teacher as he was a research scientist, Ernest Brown Babcock had an unusual education and early career that eventually led him to the new area of genetics.[8] He was born in Edgerton, Wisconsin, and expressed an early interest in flowers and gardening, growing new varieties he had ordered from seed catalogues in his own flower garden. He enrolled in Lawrence College in Appleton for one year, where he met Harley P. Chandler, a fellow plant-lover who became a lifelong friend. In 1896, however, his parents moved to California, where he attended the Normal School for two years and then spent three years teaching grammar school, a decision he soon regretted. Babcock maintained an interest in plant life in all its manifestations, wild and cultivated, which intensified in 1900 when he accompanied University of California (UC) botanists Harvey Monroe Hall and Harley P. Chandler (who also had moved to California) on a field trip to the Sierra Nevada mountains. Although he was hired on as a cook, Babcock had the chance to see professional botanists at work in the field, an experience that left him determined to pursue seriously the study of plants. The trip also helped to solidify what would be a lasting friendship that developed among these three men, which led to a number of subsequent field trips and collaborative ventures. (Fig. 1)

8. Ernest Brown Babcock, "How I Became a Geneticist," *California Monthly*, Jun 1945, 27. See also G. Ledyard Stebbins, "Ernest Brown Babcock, 1877–1954," *Madroño* 13 (1955): 81–83; G. Ledyard Stebbins, "Ernest Brown Babcock," *Biographical Memoirs of the National Academy of Science,* vol. 32 (1961), 50–66; G. Ledyard Stebbins, Holmes, *Dictionary of Scientific Biography* (ref. 7), 42–43. See also Ernest Brown Babcock, *The Genus Crepis, I and II*: *University of California Publications in Botany,* vols. 21 and 22 (Berkeley: University of California Press, 1947).

FIG. 1 Botanizing in California. Photograph of Harley P. Chandler, Harvey Monroe Hall, and Ernest Brown Babcock. Courtesy of TBL, University of California, Berkeley.

In 1901, Babcock decided to become a professional plant breeder, and approached Luther Burbank, the celebrated breeder and "plant wizard," for advice. Burbank instructed him to thoroughly acquaint himself with whatever plant material he worked with before beginning any breeding program, advice that Babcock was to follow diligently throughout his career. He enrolled at the University of California's College of Agriculture, but was disappointed to discover that there was little in the way of formal instruction in plant breeding. He followed the technical curriculum in agriculture and took all the available botany courses. In 1903 his interests appreciably widened when he attended a lecture by the Dutch plant geneticist and proponent of the popular "mutation theory," Hugo de Vries, then touring the United States.[9] Though Babcock had a hard time comprehending all of the lecture because of de Vries's thick accent, he was fired up by knowledge of the new science of genetics and by the evolutionary implications of the mutation theory.

9. For more details on the reception of de Vries's theory, see Garland E. Allen, "Hugo de Vries and the Reception of Mutation Theory," *JHB* 2 (1969): 55–88. For an examination of the reception of Mendel, the new science of genetics, and the wider agricultural context in America, see Diane B. Paul and Barbara A. Kimmelman, "Mendel in America: Theory and Practice, 1900–1919," in *The American Development of Biology,* ed. Ronald Rainger, Keith R. Benson, and Jane Maienschein (Philadelphia: University of Pennsylvania Press, 1988), 281–310.

Evolution, as it was formulated at the turn of the century, moreover, also stoked the religious fires burning in the young man. A deeply devout Congregationalist, Babcock interpreted evolution as the successive evolution of more varied forms of life, providing him with proof of the Creator's master plan. The powerful links among plants, genetics, evolution, and an undergirding religious perspective were thus forged early, and continued to motivate him for the entirety of his career.[10]

The courses in botany and later in plant pathology that Babcock had taken prepared him for his first position immediately upon graduation in 1905, teaching agricultural education to teachers-in-training. He dropped that job without hesitation, though, when he was offered the chance in 1907 to return to the University of California as the first resident employee of the Citrus Experiment Station in Riverside and then Whittier. While at the Citrus Experiment Station, he performed a series of hybridization experiments on peaches that led to the development of a popular white peach, "Babcock," that flourished in warmer climates. In 1908 he transferred to the Berkeley campus to teach plant pathology and began work on hybridization in black walnuts. In 1910 Babcock's background in agricultural education led to an invitation to organize the Division of Agricultural Education at UC, which he accepted, while continuing his breeding studies with both peaches and walnuts. This work only increased his interest in the theoretical aspects of plant breeding and in the newer area of genetics, so he continued to improve himself by taking courses, including one in heredity offered by Harry Beal Torrey in the zoology department.[11]

E. B. BABCOCK AND THE NEW DIVISION OF GENETICS (1913)

In 1912, the new dean of the College of Agriculture and director of the Agriculture Experiment Station, Thomas Forsyth Hunt, offered a series of novel opportunities to Babcock. Hunt had in mind four active divisions in his

10. Babcock's religious background and its influence on his science is discussed in G. Ledyard Stebbins, "Babcock, 1877–1954" (ref. 8). See also Williston Wirt, "Ernest Brown Babcock: An Appreciation," undated, CAS, Folder E. B. Babcock. Wirt was the minister of North Congregational Church, Berkeley, CA; Babcock was his parishioner.

11. Babcock's formal training stopped there. He did, however, continue his studies into heredity in walnuts and submitted a paper for his MA thesis which was accepted in spring of 1912. He extended this research to include questions into the nature and cause of mutations in varieties of walnuts and obtained his PhD at UC in 1916. There is some indication that Babcock felt impeded by the absence of formal training at an earlier time. See for example a letter quietly reminding Dean Hunt of his credentials and indirectly requesting promotional considerations. E. B. Babcock to Thomas F. Hunt, 2 Dec 1912, EBB, Folder Letters Written by Babcock, 1909–1949. For more on Babcock's early struggles with the UC administration see Kimmelman, "Progressive Era" (ref. 5).

college: Agricultural Chemistry, Soils, Plant Propagation, and Principles of Breeding Plants and Animals. Hunt considered the latter category to play a special role in the instruction of agriculture because it was as "as fundamental as the English language" to agricultural instruction.[12] Babcock, who realized that his lifelong ambition to pursue plant breeding full-time was now possible, volunteered with Hunt's hearty approval to organize the division under the novel name of "Genetics," the first such formal academic unit to take that name in the United States. Babcock remained its head until 1947.

Although organizing the new division took a great deal of his time, Babcock's position was formally split between research and the development of a course that he had long dreamed of teaching, namely plant breeding. Most important, running the division also enabled him to pursue his growing interest in genetics, an area he began to promote with a vengeance. He wasted no time redefining the mission of the division in terms of genetics, pointing out that plant breeding was grounded on the principles of the new science. In the first report of his Division in 1913 which Babcock began to use as the mission statement: "Genetics is a recently recognized branch of biological science. The principles of the future science of breeding are being formulated by the geneticists of the present. It is the purpose of the Division of Genetics to conduct original investigations in the study of variation and heredity."[13] He also rapidly converted his assigned plant breeding course to a full-blown introductory genetics course—Genetics I.[14]

In 1914 Babcock hired Roy Elwood Clausen, with whom he eventually published an influential textbook in 1918 titled *Genetics in Relation to Agriculture.*[15] It was the first such textbook in existence and was used widely in the 1920s and 1930s; one colleague, Princeton geneticist George Harrison Shull, congratulated him on "far and away the best genetical text-book in existence. Every teacher of genetics certainly owes you a debt of gratitude and you will find them repaying it when your royalties come in."[16] A revised and expanded edition, appearing in 1927, continued to be successful. In 1918 Babcock also wrote a successful Genetics Laboratory Manual for instructional purposes with Julius

12. University of California, College of Agriculture, *Record of the Dedication* (ref. 4), 37.

13. It is unclear precisely when Babcock deleted the second sentence outlining the relationship of plant breeding to genetics. Given other indicators, it is likely he did this shortly after 1913. "Division of Genetics: Report to the Director of the Experiment Station," 13 Jun 1913, EBB, Folder Division of Genetics of the Department of Agriculture. See also mission statement in "Department of Genetics," 7 Apr 1956, JAJ (ref. 1).

14. "Teaching Materials," EBB, Folder Materials Regarding the Division of Genetics.

15. Ernest Brown Babcock and Roy E. Clausen, *Genetics in Relation to Agriculture* (New York: McGraw Hill, 1918).

16. George Harrison Shull to E. B. Babcock, 29 Apr 1918, JAJ (ref. 3).

L. Collins, a plant geneticist he appointed to the division and an eventual collaborator on the *Crepis* program.[17]

Once his position and teaching duties were under control, Babcock began to look for a suitable research project that would sustain his interest in plant genetics. From 1914 to 1918, Babcock was closely following the work of Thomas Hunt Morgan's *Drosophila* program. He greatly appreciated the insights emerging from this research program, but also knew enough about the differences between species to seek corroborative evidence from organisms other than *Drosophila* before fully accepting that Morgan's ideas were universally applicable. He observed the urgency for the person "who allies himself with those biologists who believe in the present importance and future promise of this collection of genetic evidence, derived as it is, almost entirely from a single species of insects, to consider most carefully the selection of other material with which to test the various hypotheses that have been proposed in order to interpret the great mass of drosophila data consistently."[18]

Babcock thus began to consciously search for a plant counterpart of *Drosophila* in order to corroborate the data emerging from the Morgan group. As his 1913 division report observed, "Both plants and animals have certain advantages and disadvantages as materials for use in the study of genetic problems. Hence the student of genetics must be ready to resort to the use of any living organism that gives promise of revealing the natural laws upon which the future science of breeding will be grounded."[19] Thus, the plant material chosen for genetical investigation did not necessarily need to have an agricultural application; the principles of plant genetics could not be subordinated to the use of plants for human needs, and that freed him to choose any suitable plant he could find.

THE DESIDERATA OF "THE IDEAL FORM" FOR GENETICS AND THE SEARCH FOR A PLANT COUNTERPART OF *DROSOPHILA*

The most suitable organism for genetical study, Babcock knew, needed to meet a number of important criteria. He articulated these in an article published in 1920 in the way of desiderata for the "ideal form for genetic investigations."

17. A copy is deposited at APS.

18. Ernest Brown Babcock, "*Crepis*—A Promising Genus for Genetic Investigations," *American Naturalist* 54 (1920): 270–76, on 270.

19. "Division of Genetics: Report to the Director of the Experiment Station," 11 Jun 1913, EBB, Folder The Division of Genetics of the Department of Agriculture. See also the mission statement of the Division "Department of Genetics," JAJ (ref. 1).

This organism had to have a low chromosome number; to display "numerous germinal variations"; to be tractable, easy to grow in laboratory or greenhouse conditions with abbreviated life cycles; and to produce numerous progeny. For plants, the ideal form had to be both self-fertile to establish pure lines, and lend itself easily to hybridization.[20]

Babcock knew that no plant species could possibly compete with most insect species, which had brief life cycles, but he also recognized that plant material had some notable advantages. Since plants could reproduce vegetatively, lines of stocks could be maintained for future reference, and unlike animals, plants could be readily hybridized, a critical feature. Babcock here saw an opportunity to follow up on an important directive issued by Morgan in his 1919 book, *The Physical Basis of Heredity:*

> The theory that the chromosomes are made up of independent self-perpetuating elements or genes that compose the entire hereditary complex of the race, and the implication contained in the theory that similar species have an immense number of genes in common, makes the numerical relation of the chromosomes in such species of unusual interest. This subject is one that could best be studied by intercrossing similar species with different numbers of chromosomes, but *since this would yield significant results only in groups where the contents of the chromosomes involved were sufficiently known to follow their histories,* and since as yet no such hybridizations have been made, we can only fall back on the suggestive results that cytologists have already obtained along these lines.[21]

Babcock added, "It is not sufficient that the species have low numbers and different numbers; it is also necessary that the inheritance of a sufficient number of characters in each species be studied so as to establish the linked groups of characters or genes corresponding to the chromosomes of each species. Only then can the contents of the chromosomes involved be sufficiently known to follow their histories in the hybrids."[22]

The qualifier shaped Babcock's search for a plant counterpart to *Drosophila* with low chromosome numbers that would fulfill as many of the desiderata as possible. He began with the intention of examining the chromosome number

20. Babcock, "*Crepis*" (ref. 18), 271.

21. Quoted in ibid., 272. The italics were added by Babcock. The quoted entry also had a transcription error leaving out the phrase "on the cytological possibilities involved, and on the suggestive results that cytologists have already obtained along these lines." See Thomas Hunt Morgan, *The Physical Basis of Heredity* (Philadelphia: J. P. Lippincott and Co., 1919), 147.

22. Babcock, "*Crepis*" (ref. 18), 272.

in *Hemizonia*, a genus of the Madiinae commonly known as the hayfield tarweeds, assisted by his old friend and current Berkeley colleague, Harvey Monroe Hall. A letter to George Harrison Shull dated September 23, 1915, reveals how he came across the genus *Crepis*:

> It may be that *Crepis virens* will prove to be a much more satisfactory subject for our work than *Hemizonia,* as I learn from East's recent paper that it has only six chromosomes. I am already taking steps to secure seeds of this species from as many different localities as possible. If you can give me any assistance in doing this I shall be very grateful. Will be glad to get names of parties who might assist me in various parts of the world. I find that we have herbarium specimens from Berkeley, Sierra Nevada Mountains, Vancouver Island, Whidby Island, Humboldt County, California; Upper Austria, and, I believe, Germany. Some of the Austrian and German specimens were so very distinct as to look like different species. They were small plants (perhaps young), but with peculiar, almost entire leaves and few heads. Do you know whether anyone else is carrying on breeding investigations with this species?[23]

Shull's answer, dated September 30, 1915, responded no to this last query. Shull then added: "I suppose you do not know whether parthenogenesis takes place in this species. The small number of chromosomes should make this valuable material for genetic studies, provided the breeding habits are of such a nature as to make its technique sufficiently simple."[24] That caveat was to prove prophetic. The genus was anything but simple in its breeding habits, using a variety of means to reproduce. (*Crepis* is in fact a close relative of *Hieracium*, commonly known as the hawkweed, the same genus that had defied Mendel's attempt to apply the principles he had derived from *Pisum sativum*.) Little was actually known about *Crepis,* and the only work on it to that point had been to determine the chromosome number in some species by European cytologists such as H. O. Juel, Otto Rosenberg, L. Digby, and a young, especially promising Russian cytologist named Michael Navashin (son of the cytologist Sergey Navashin), who had published the most recent chromosome counts on the genus in 1915. Their work confirmed the low and varying chromosome number in a number of species of *Crepis*. This knowledge (and encouragement from Michael Navashin and others) gave Babcock confidence in his choice of

23. E. B. Babcock to George H. Shull, 23 Sep 1915, UCGD, Folder University of California Division of Genetics Papers, Babcock to George H. Shull 1911–1942.

24. George H. Shull to E. B. Babcock, 30 Sep 1915, UCGD, Folder University of California Division of Genetics Papers, G. H. Shull to Babcock 1914–1918.

organism for genetical study, "one of my correspondents going so far as to predict that in time *Crepis* will become as famous and useful for laboratory work as *Ascaris* is to-day."[25]

Crepis possessed other favorable traits. The genus showed great morphological variation and a very wide distribution with both Old World and New World forms that included annual, biennial, and perennial species, with a broad preference of environments from deserts to swamps, meadows, seashores, and alpine habitats. According to the celebrated botanical authority, the Index Kewensis, the genus was very large, with nearly 200 recognized species. Some of the species had been successfully hybridized and some of the plants could easily be grown in greenhouse conditions. Because of all these considerations, Babcock was convinced of the worthiness of *Crepis*: "Sufficient has been said, I trust, to convince the reader that we have in *Crepis* a wealth of material which may fairly be expected to furnish data of the greatest value in testing the generality of the chromosome theory of heredity, and that this group is unique in the promise it holds of carrying out that test in much shorter time than would be required if we should depend only on the data which is closely accumulating from other plants now under investigation."[26]

FROM GENETICS TO EVOLUTION: THE EVOLUTION OF A RESEARCH PROGRAM

The work began in earnest in 1915. Babcock's early studies through 1922 mainly determined chromosome number (usually from root tip cells or seeds) or experimented with hybridization. Babcock began slowly with seeds that he grew as garden cultures from two species obtained from both botanical gardens and from the wild. From these he selected plants with variable characters promising for further study and performed crosses on them. These hybridization experiments raised critical questions about the processes of evolutionary change under debate at the time; specifically, the question of which of the two known processes of evolutionary change, gene mutation (favored by Morgan and de Vries) or hybridization (favored by J. P. Lotsy and others), was more important in the evolution of the genus. After performing a range of crossing experiments, Babcock concluded that both played an important role in the evolution of the

25. Babcock, "*Crepis*" (ref. 18), 274.
26. Ibid., 275.

genus, but that in addition, Lamarckian inheritance—the bane of plant evolutionists at the time—could not be ruled out.[27]

The genus thus initially appeared very promising for genetic and evolutionary study, and Babcock continued to increase his collections through an extensive network of fellow collectors from all over the world, obtaining seeds and roots of known species from both cultivated and wild contexts. These were grown in garden cultures on the Berkeley campus, compared to existing herbarium specimens, examined cytologically, and hybridized with other species. The progeny, if any, were then examined morphologically and cytologically and followed closely.

The nature of the *Crepis* project changed dramatically in the early 1920s, however, when a number of critical problems were encountered. Generation times were longer than hoped for and the plants required more growing space; some required specialized soils, and the long slender, woody roots that enabled some of the species to flourish on mountainsides made transplantation difficult. Even more disappointing, was the fact that the kinds of linkage and types of mapping studies performed in *Drosophila* proved themselves difficult in the plant. As Babcock's accessions of species in the genus and all their close relatives increased, moreover, it became apparent that the entire group was in complete taxonomic confusion; before *any* genetic study could be done, the taxonomy of the nearly 200 known species had to be worked out. Thus, in part because *Crepis* proved intractable to classical genetic study, and in part because it also required detailed systematic study as a preliminary to any other, Babcock gradually reoriented his research program in the direction of systematics—but it was a new kind systematics, a systematics that assimilated genetical knowledge.

To begin a proper systematic study of the genus, Babcock relied again on his Berkeley colleague and collaborator, Harvey Monroe Hall. Together with ecologist Frederic Clements, Hall had been urging taxonomic reform at this time, against a great deal of opposition. Their joint publication of 1923, *The Phylogenetic Method in Taxonomy*, was a kind of taxonomic manifesto, amounting to an overhaul of the existing, largely static taxonomic system that focused exclusively on the morphological characters located on herbarium specimens;[28]

27. Ernest Brown Babcock, "Species Hybrids in *Crepis* and Their Bearing on Evolution," *American Naturalist* 58 (1924): 296–310.

28. Harvey Monroe Hall and Frederic E. Clements, *The Phylogenetic Method in Taxonomy* (Washington, DC: Carnegie Institution of Washington, publ. no. 326, 1923).

their method stressed evolutionary or phylogenetic relationships and depended instead on experimental studies that included tools and insights from ecology and genetics.[29] Babcock embraced Hall's systematic preferences and collaborated with him on a detailed study of variation in the genus *Hemizonia congesta.*[30] As he reminisced in 1947: "it was Hall's emphasis on the phylogenetic viewpoint in taxonomy which led [me] to undertake, with the aid of various co-workers and students, the investigations on the genetics and cytogenetics of *Crepis* which have made possible the present attempt at a phylogenetic treatment of this genus."[31] This emphasis on experimental approaches that examined patterns in variation and processes that were responsible for it, using tools and insights from ecology, genetics, cytology, and biogeography, was part of the "new systematics" (as Julian Huxley named it) that was emerging at that time.[32]

Indeed, Babcock and Hall, along with *Crepis* workers in the 1930s, would lead the way to formulating what came to be called biosystematics, an evolutionary and interdisciplinary movement in taxonomy in the 1940s, and contributed to its dominance in northern California.[33] This reflected the wider integration of Mendelian genetics with Darwinian evolutionary theory. Babcock and his research program were to play critical roles in the historical event later known as the "evolutionary synthesis."[34] In 1934, for instance, he organized the

29. Joel B. Hagen, "Experimentalists and Naturalists in Twentieth-Century Botany, 1920–1950," *JHB* 17 (1984): 249–70; Vassiliki Betty Smocovitis, "Botany and the Evolutionary Synthesis: The Life and Work of G. Ledyard Stebbins Jr." (PhD dissertation, Cornell University, 1988); Vassiliki Betty Smocovitis, "Disciplining Botany: A Taxonomic Problem," *Taxon* 41 (1992): 459–70.

30. Ernest Brown Babcock and Harvey Monroe Hall, "*Hemizonia congesta*: A Genetic, Ecologic and Taxonomic Study of the Hayfield Tarweeds," *University California Publications in Botany* 13 (1924): 15–100.

31. For the connection to Hall and the rationale for the taxonomic treatment of the genus see Babcock, *Genus Crepis* (ref. 8), 13.

32. Julian Huxley, *The New Systematics* (Oxford: Clarendon Press, 1940).

33. For more background on the origin of this term and its relation to classical herbarium taxonomy see Smocovitis, "Botany and the Evolutionary Synthesis" (ref. 29); Vassiliki Betty Smocovitis, "G. Ledyard Stebbins and the Evolutionary Synthesis (1924–1950)," *American Journal of Botany* 84 (1997): 1625–37; Vassiliki Betty Smocovitis, "Keeping Up with Dobzhansky: G. L. Stebbins, Plant Evolution and the Evolutionary Synthesis," *History and Philosophy of the Life Sciences* 28 (2006): 11–50.

34. For more on the synthesis, see Ernst Mayr and William B. Provine, eds., *The Evolutionary Synthesis: Perspectives on the Unification of Biology* (Cambridge, MA: Harvard University Press, 1980); Vassiliki Betty Smocovitis, *Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology* (Princeton: Princeton University Press, 1996).

first meeting that formally brought together geneticists, systematists, and paleontologists to discuss principles of evolution as they existed at the time, fully five years before the celebrated American Association for the Advancement of Science meetings that launched the Society for the Study of Speciation, the precursor to the Society for the Study of Evolution.[35] Later still, Babcock served as Chair of the Western Group of the Committee for Common Problems in Genetics, Paleontology, and Systematics, organizing an important meeting in the Bay Area in 1943, and participating as a discussant in the mimeographed bulletins of the Committee for Common Problems of Genetics, Paleontology, and Systematics.

What began as a corroboration and extension of Morgan's *Drosophila* program was therefore converted into a vastly more inventive and ambitious phylogenetic and evolutionary study of a plant genus that fully embraced available genetical knowledge—the first such study seriously attempted in plants. No longer was its goal to corroborate the program launched by Morgan on *Drosophila*; it instead sought to answer fundamental questions on the origin of species, the long-desired holy grail of Darwinian evolution. Questions pertaining to hybridization, variation patterns, and the processes that gave rise to them, speciation mechanisms, along with the ultimate goal to "create new species," increasingly came to dominate Babcock's thinking about his research program.[36] The systematic work was such a great undertaking that it quickly became the primary goal of the *Crepis* program: that is, as Babcock succinctly

35. As Babcock described it in a letter, "I am wondering whether anything can be done in the way of interpreting the paleontological processes in terms of modern genetical concepts. What I am thinking of is a symposium which might be entitled 'Evolutionary Processes,' with perhaps three topics somewhat as follows: (1) evolutionary processes in plants; (2) evolutionary processes in animals; (3) interpretation of the paleontological record in the light of cyto-genetical concepts." E. B. Babcock to A. Franklin Shull, 6 Feb 1934, UCGD, Folder Babcock to A. Franklin Shull, 1934. For more on the precursor societies leading to the Society for the Study of Evolution see Vassiliki Betty Smocovitis, "Organizing Evolution: Founding the Society for the Study of Evolution," *JHB* 27 (1994): 241–309. There is some indirect evidence pointing to Babcock's attempt to bring systematics, genetics, and paleontology together as early as 1932.

36. Ernest Brown Babcock, "Investigations in the Genus *Crepis*," in *Carnegie Institution Yearbook*, 25, 1925–1926 (Washington, DC: Carnegie Institution of Washington, 1926), 316. The realization that interspecific hybridization might be facilitated by spontaneous chromosome doubling led investigators to the promise of creating new species. In 1927, the Russian G. D. Karpechenko designated the hybrid he artificially generated between a radish and a cabbage as *Raphanobrassica,* a "species nova" or new species. See G. D. Karpechenko, "Polyploid Hybrids of *Raphanus sativus* L. x *Brassica oleracea* L.," *Bulletin of Applied Botanical Genetics and Plant Breeding* 17 (1927): 305–410.

FIG. 2 E. B. Babcock collecting *Crepis*. Courtesy of G. Ledyard Stebbins. In author's possession.

defined it in 1928, to obtain "a clearer understanding of the evolutionary processes at work in this group of about 200 related species."[37] In taking this direction, of course, Babcock was fulfilling his early interest in genetics and evolution as he had first encountered them in 1903 from de Vries; he was also quietly realizing his personal wish for a progressive evolution that grounded his faith.

Babcock was simultaneously fulfilling his own early love of plants by retooling in the techniques of classical herbarium taxonomy, floristics, biogeography, and even plant hunting and collecting. (Fig. 2) He spent 1924–1925 working in herbaria outside the University of California, including European herbaria and the Gray Herbarium at Harvard (where he was headquartered for five months) to study available type specimens and other critical materials. At the same time, Babcock and his associates launched a series of collecting expeditions for living specimens (usually the seeds, roots, flower heads, or entire

37. Ernest Brown Babcock, "Investigations in the Genus *Crepis*" (Washington, DC: Carnegie Institution of Washington, publ. no. 29, 1928), 352.

plants pressed in the field) from the western U.S. In 1930 Babcock undertook a five-month expedition to collect *Crepis* in the Mediterranean. The grueling itinerary included collecting stops in Madeira, Portugal, Spain, Morocco, Algeria, Tunisia, Sicily, Italy, Greece, and Crete.[38] At each place, Babcock not only increased his stock of *Crepis*; he also made crucial contacts with collaborators and collectors who would continue to send him materials and personnel as needed.[39]

GROWING THE *CREPIS* RESEARCH PROGRAM

With the scope of the project expanding to include the systematics and evolution of the genus, the collaborators, assistants, and students required to make the project successful also began to increase in number and broaden in expertise. As head of the genetics division, from the outset Babcock had access to internal assistance from the college and the university in the matter of salaries, research funds, laboratory, garden, and greenhouse space, and even publication venues such as the University of California Press, which published his major monographs. He obtained extensive support especially from the California Agricultural Experiment Station, which funded the program continuously from 1918 on; the Experiment Station had officially recognized it as a major project in the Division of Genetics.[40] Funding increased further as the project began to delve into the exciting new areas of experimental taxonomy and experimental evolution.[41] These new areas were ac-

38. See Babcock, *Genus Crepis* (ref. 8), 3.

39. See the list of acknowledged contacts in ibid., 29.

40. Ibid.

41. The best source describing the goals and objectives of experimental taxonomy and evolution is a report written by Jens Clausen sometime in the early 1930s. On pages 1–2, he wrote: "The objectives of this program in experimental taxonomy are to further the understanding of the evolution, the differentiation, and the interrelationships of plant life. We emphasize that it is all the various relationships of kinships of plant life we wish to study; the morphologic, cytologic, genetic, distributional, ecologic, and eventually anatomic and physiologic relationships, as well as the responses of plant life to its environment. Wherever possible, our approaches to these problems are by experimental methods, or we try to be on the alert for those experiments which nature has performed in the field. Because of the emphasis on experiment and relationship, the name Experimental Taxonomy is used for this line of research." Jens Clausen, "Experimental Taxonony: Objectives, Facilities, and Methods," CP, Folder Methods in Experimental Taxonomy I. A second report written at a later date builds on this: Jens Clausen, "Experimental Taxonony: Objectives, Facilities, and Methods," CP, Folder Methods in Experimental Taxonomy I. See also Hagen, "Experimentalists" (ref. 29).

tively encouraged by the Carnegie Institution of Washington, which granted Babcock an additional thousand dollars annually, supplementing his regular support from the California Research Board.[42] These funds were used to support research, and by the late 1920s, Babcock had been, or was actively collaborating with, colleagues, assistants, and students on the project that included Julius L. Collins, Margaret C. Mann, Lillian Hollingshead, and Priscilla Avery.[43]

The number of women researchers in the project was striking, though not unexpected in a field that was supplanting traditional botany, an area with a precedent for attracting women to science.[44] Some of these women were illustrators and artists, along with the typists who remained largely invisible in the publications.[45] Babcock played an active role supervising the research, but tended to avoid the kinds of routine cytological or experimental hybridization studies that were left to his many associates, assistants, and students. His intellectual contribution to the project, especially evident in the publications, was to interpret their findings, especially with regard to the big picture of plant evolution, which he increasingly seemed to relish.[46] The *Crepis* program was in actuality a large cooperative of students (many of whom, such as Collins and eventually Donald R. Cameron, received their training in, and then were hired by, the same Division), faculty, assistants, and visitors to the campus, all working under Babcock, who in turn served

42. On the CIW grant see the contents of the two folders devoted to the subject with correspondence between E. B. Babcock and officials at CIW: RG, Box 12, Folders 175 and 176, University of California–Plant Genetics, 1931–1935.

43. In the 1930s, Babcock also collaborated with Olive Swezy, S. L. Emsweller, and Marion Cave. Other women students contributing to the project included Marta Sherman Walters, A. M. R. Burns, Helen Carlyle, and Mrs. Homer Perry Sherman. Avery and Cave had also been Babcock's students.

44. See Margaret Rossiter, *Women Scientists in America: Struggles and Strategies to 1940* (Baltimore: Johns Hopkins University Press, 1982). See also Margaret Rossiter, "Sex Segregation in the Sciences: Some Data and a Model," *Signs* 4 (1978): 146–51; Margaret M. Rossiter, "Which Science? Which Women?" *Osiris* 12 (1997): 169–86. For a more recent treatment directly bearing on the history of genetics see Michael R. Dietrich and Brandi H. Tambasco, "Beyond the Boss and the Boys: Women and the Division of Labor in *Drosophila* Genetics in the United States, 1934–1970," *JHB* 40 (2007): 509–28. Babcock's group showed a comparable division of labor.

45. Two such illustrators in the *Crepis* project were Mrs. Katherine Jenkins (the wife of James Jenkins) and Miss Anna Hamilton. Other work by women included tasks like seed collecting and emergency typing. See E. B. Babcock to H. A. Spoehr (undated but likely 1936), CP, Folder Correspondence, Dr. E. B. Babcock Through September 11, 1946. Babcock also employed individuals to culture plants and grow them under diverse conditions. On occasion Babcock also employed translators since many of the scientific texts were in German or Russian.

46. The publications coming out of the *Crepis* project reflected this trend.

as mentor, facilitator, and interpreter of the data they generated, especially with respect to evolution.[47]

Babcock also was known for his generous support of capable researchers. He mentored and zealously recruited younger people and scholars to his program from all over the world.[48] He went to great lengths to help place his students and assistants, sometimes retaining them at Berkeley or nearby in the Bay Area. His laboratory was open to visitors from all over the world. The Danish genecologist Jens Clausen stayed some eight months with the *Crepis* team in 1927–1928, gaining further expertise in cytogenetics. The English geneticist M. M. Richardson and Swedish plant geneticist Arne Müntzing visited later, in the early 1930s. Even John Belling, by then a famously antisocial plant geneticist, found a temporary home under Babcock's wing on the genetics of *Crepis* in the late 1920s (though Babcock privately viewed him as a fundamentally uncooperative co-worker).[49] Babcock also developed especially close ties with Morgan's group in Pasadena, inviting workers such as H. J. Muller, Curt Stern, and other students and visitors from Morgan's lab to Berkeley. He opened communication channels with drosophilists located there and the genetics community all over the world. (Fig. 3)

In 1927 Babcock was able to help bring Michael Navashin to the Berkeley campus on an International Education Board Fellowship.[50] Navashin arrived with a series of unusual *Crepis* mutants, some of which had been induced with x-rays or others which had mutated naturally through aging, and with his

47. In this sense, it closely resembled its contemporary genetics cooperatives in Morgan's *Drosophila* and Emerson's maize research programs. See Kohler, *Lords of the Fly* (ref. 7); Lee B. Kass et al., "Cornfests, Cornfabs and Cooperation" (ref. 7). The nature of the collaborations and the group dynamic was recognized by Babcock and his group. See, for example, the list of persons included and the new proposal to build physiological genetics on the UC campus. "List of Faculty," 13 Aug 1945; also "Memo: To Members of the Faculty of the University of California Who Are Actively Interested in the Fundamental Problems of Physiological Genetics," 13 Aug 1945, both in JAJ, Folder E. B. Babcock.

48. Stebbins, "Babcock, 1877–1954" (ref. 8); Stebbins, "Babcock," *Biographical Memoirs* (ref. 8).

49. See the various correspondence on John Belling by Babcock: CP, Folder E. B. Babcock (ref. 45). Belling's "tragic mental affliction" was discussed at the time of his death as were charges that he was "mentally deranged." Rumors had spread on the East Coast that Belling had committed suicide. Babcock was quick to respond to such rumors by making the coroner's report public. His death on July 23, 1933 was due to heart disease. See Robert C. Cook to E. B. Babcock, 13 Aug 1933; his handling of one difficult report on Belling in E. B. Babcock to H. A. Spoehr, 22 Aug 1933; E. B. Babcock to H. A. Spoehr, 27 Jul 1933; E. B. Babcock to H. A. Spoehr, 15 Sep 1932, all in CP (ref. 2).

50. Ernest Brown Babcock to Michael Navashin, 11 Oct 1927, UCGD, Folder University of California Genetics Department, Babcock to M. Navashin, 1927.

FIG. 3 Photograph of Ernest Brown Babcock, Curt Stern, and Thomas Harper Goodspeed dated 1933. Courtesy of TBL, University of California, Berkeley.

own extensive expertise gained from the renowned Russian school of cytogenetics.[51] Navashin stayed for nearly three years, earning a PhD while collaborating with Babcock. In 1930 Babcock and Navashin published the first monographic treatment of the genus, applying the methods of taxonomy, cytology, and genetics in the group.[52] The final section of the monograph was devoted to discussion of the evolutionary processes operating in the genus. After a detailed exploration of available evidence, they postulated that three

51. The Russian school of cytogenetics included workers like his father Sergey Gavrilovitch Navashin, who discovered the phenomenon of double fertilization in 1898; G. A. Lewitsky and N. P. Avdulov, who constructed the first karyotype in the Gramineae; and Michael Navashin and his contemporary Helen Gerassimova, who induced mutants in *Crepis* by the use of x-rays or through natural processes such as aging.

52. Ernest Brown Babcock and Michael S. Navashin, "The Genus *Crepis*," *Bibliographia Genetica* 6 (1930): 1–90.

fundamental processes could account for evolutionary change: point mutations (or genic alterations in individual genes); chromosomal changes in number and morphology; and interspecific hybridization. Although these three processes were evidently operating in the genus, Babcock and Navashin could not at that point determine which was the most important; all three contributed "something to the origin of species."[53] When Navashin's fellowship ran out, Babcock expended enormous energy to retain him in the United States, and in the Bay Area, but he was ultimately unsuccessful.[54]

By 1934 Babcock had accumulated enough evidence to sort out the relative importance of various genetic processes in the evolution of genus. Evolution in *Crepis* was not only the result of gene mutation, but also the transformation of an ancestral 10-chromosome form to derivative 8- and 6-chromosome forms. Since gene mutation alone could not account for this kind of change, Babcock suggested that the reduction in chromosome number possibly came about through a process of reciprocal translocation between nonhomologous chromosomes. His observations, however, placed him at odds with the new understanding that was emerging from theoretical population genetics in the work of R. A. Fisher, Sewall Wright, and J. B. S. Haldane.[55] Fisher and Wright preferred gene mutations, but not Haldane, who had some experience with plant genetics and appreciated chromosomal effects. In a benchmark overview of genetic evolutionary processes operating in *Crepis* that appeared in the *Proceedings of the National Academy of Sciences* in 1934, Babcock observed: "To what extent a mathematical theory of natural selection can be applied to the results of these other categories of genetic change remains for the future to disclose."[56]

53. Ibid., 76.

54. There is extensive correspondence that includes letters and shipboard telegrams (Babcock was traveling to Europe) pertaining to Navashin's retention. See especially the telegrams sent from the steamship Majestic: Ernest Brown Babcock to H. A. Spoehr, 22 Apr 1930; and Alice E. Buckner to Herman A. Spoehr, 23 Apr 1930, both in CP (ref. 49). And see the letters: E. B. Babcock to H. A. Spoehr, 5 May 1930; H. A. Spoehr to E. B. Babcock, 8 May 1930; E. B. Babcock to H. A. Spoehr, 31 May 1930; E. B. Babcock to H. A. Spoehr, 30 Jun 1928, all in CP (ref. 49); and E. B. Babcock to E. D. Merrill, 19 Sep 1928, UCGD, Folder Babcock to E. D. Merrill, 1928. It is unclear what role Harvey Monroe Hall played in Navashin's retention. In a letter to H. A. Spoehr he expressed reservations about retaining Navashin over hiring other geneticists like Francis Blakeslee. He also viewed Navashin's work as peripheral to his own. See Harvey Monroe Hall to H. A. Spoehr, 21 Jul 1928, CP, Folder Hall, Dr. H. Navashin eventually returned to the Soviet Union.

55. See Provine, *Origins* (ref. 7) and Provine, *Sewall Wright* (ref. 7) for their individual views of evolution in Mendelian populations.

56. Ernest Brown Babcock, "Genetic Evolutionary Processes," *Proceedings of the National Academy of Sciences* 20 (1934): 510–15, on 514.

In 1934 Babcock expanded the scope of the *Crepis* program still further, launching a detailed study of the geographic distribution of the genus and its related genera. This geographic study in turn led him to study the closest relatives of *Crepis* to gain insight into the origins of the group.[57] This expanded project added to the administrative burdens he was already shouldering, and Babcock foresaw that with retirement on the horizon (he was fifty-seven), he would require both extra hands and additional expertise if the research program were to be completed; it already seemed to be ballooning out of his control. He applied to the Rockefeller Foundation for a grant to fund the expansion of the project. Earlier, in 1931, Herman A. Spoehr, Director of the Natural Sciences at the Rockefeller Foundation, had declined even to entertain a formal application from Babcock on the grounds that "this type of endeavor lies in a field in which the Foundation has at present no special program which would warrant formal consideration."[58] But under the new director, Warren Weaver, Babcock was able to secure the sum of $12,000 over the course of three years, $4,000 of which was to fund the salary for two researchers.[59] This was in addition to the Carnegie Institution's annual contribution of $1,000, the annual allotment of $500–1,000 that the California Research Board provided, and the University's commitment of $5,000 per year to "salaries, supplies, and facilities" for the duration of the Rockefeller grant.[60]

Babcock's grant application requested two assistants. One was to perform routine cytological counts, while the second would work more closely on the cytology and systematics of the relatives of *Crepis*. The first position, with the smaller salary of $1,500, was filled by James Jenkins, a recent Berkeley graduate who had worked with Babcock previously. The second position for a "junior geneticist" required more expertise and knowledge of the Compositae, the daisy or dandelion family, of which *Crepis* was a member; for that reason it had a salary of $2,500. Babcock hired George Ledyard Stebbins Jr., a young professor of botany at Colgate University. Stebbins was a recent graduate of Harvard University, formally trained in systematic botany and cytology and whose interests had turned in the 1930s to the cytogenetics of the Compositae. He

57. For the rationale see Jens Clausen, "Memorandum re Babcock's Proposed New Program on the Crepidinae," 24 Sep 1934; Jens Clausen to E. B. Babcock, 24 Sep 1934; E. B. Babcock to Jens Clausen, 2 Oct 1934; E. B. Babcock to H. A. Spoehr, 8 Jul 1935, all in CP (ref. 2).

58. Herman A. Spoehr to E. B. Babcock, 15 May 1931, RG, Box 12, Folder 175 University of California–Plant Genetics, 1931–1935.

59. Warren Weaver to President Sproul, 21 Mar 1935, RG, ibid.

60. "Proposal," 15 Mar 1935, RG, ibid.

was recommended to Babcock by Sydney Blake, a Washington-based expert on the Compositae. Stebbins, in turn, was excited by the prospect of devoting himself full-time to cytogenetic study, especially on *Crepis* after having seen Babcock's poster on the evolutionary tree of *Crepis* exhibited at the 1932 International Congress of Genetics in Ithaca, New York. Despite an embarrassing attempt to leverage a higher salary (George Stebbins Sr. tried to use his friendship with John D. Rockefeller to his son's advantage),[61] Stebbins joined the *Crepis* group in the summer of 1935.[62]

THE "MECCA OF EVOLUTIONISTS": GENETICS AND EVOLUTION AT BERKELEY (1935–1939)

By 1935 Berkeley genetics was booming. A 1934 survey comprised of a jury of geneticists appointed by the American Council of Education listed seventeen universities as adequately equipped and staffed for work leading to doctorates in genetics; six of these were judged distinguished, and Berkeley was one of the six.[63] The number of geneticists at Berkeley was increasing, and with additional appointments being made in other academic units, the division increasingly saw as part of its mission the need "to integrate the activities of geneticists in other units."[64] Thomas Harper Goodspeed, who had joined the botany department in 1914 with Babcock and Clausen, and having received his degree at Berkeley, began actively collaborating with Clausen on a series of celebrated genetical experiments and on expeditions to the Andes to determine the origins of *Nicotiana tabacum,* the cultivated tobacco plant; a number of assistants and students were associated with that project. In 1934 Donald R. Cameron, yet another Babcock student and collaborator on the *Crepis* project, formally joined the division.[65]

In the Poultry Husbandry Department, Russian émigré geneticist Isadore Michael Lerner was completing his doctoral degree to join the faculty in 1936,

61. See the numerous letters negotiating the terms and condition of Stebbins's salary in RG, ibid. See also the correspondence with the Carnegie Institution in CP (ref. 2).

62. The Carnegie Institution also questioned Babcock's use of funds intended for his *Crepis* monograph (rather than the related American species of *Crepis* research) for Stebbins's moving expenses. In response Babcock wrote a series of letters to Herman Spoehr that gave a rationale and description of the new project and why it was crucial to the larger *Crepis* monograph funded by the Carnegie. See especially E. B. Babcock to H. A. Spoehr, 8 Jul 1935, CP (ref. 2).

63. "Department of Genetics," 7 Apr 1956, JAJ (ref. 1).

64. Ibid.

65. Ibid.

as was his eventual collaborator geneticist Everett R. Dempster in the genetics division.[66] While still students, Lerner and Dempster organized a group of younger Berkeley researchers with a keen interest in integrating knowledge of the new genetics in both practical and theoretical terms within the new dynamic evolutionary framework that was emerging through the efforts of theorists such as Fisher, Wright, and Haldane. This group, a fortnightly journal club, took the informal title of "Genetics Associated." By the late 1930s the group also included Jenkins, Stebbins, Cameron (then a research assistant to Roy Clausen), and plant breeders Francis Smith and Alvin Clark. Lerner's old friend, Russian émigré Theodosius Dobzhansky, was also a frequent visitor to the Bay Area while he was with the Morgan lab at the California Institute of Technology in Pasadena.[67] Dobzhansky especially infused Berkeley colleagues with his enthusiasm for evolutionary genetics as it was emerging from his researches on varied species of *Drosophila* as well as his novel synthetic insights as revealed in his 1937 book, *Genetics and the Origin of Species*.[68]

In 1939 Berkeley genetics grew even more international when the German émigré geneticist Richard Goldschmidt formally joined the zoology department, working closely with other geneticists, including Babcock.[69] In 1939, for example, Babcock and Goldschmidt collaborated on a public exhibit, one of the University of California's installations in the Hall of Science at the Golden Gate International Exposition (more colloquially known as the San Francisco World's Fair). This novel "mechanized exhibit of human heredity" demonstrated Mendelian inheritance patterns with an alternating bride and groom using "Dionne" dolls, modeled after the Canadian Dionne quintuplets and specially manufactured for the exhibit.[70] It also demonstrated Babcock's shrewd ability to teach and promote genetics to wider audiences.

The Bay Area as a whole was becoming a hub of evolutionary activity, with the Carnegie Institution of Washington team of Jens Clausen, David Keck, and William Hiesey, also known as the Carnegie Brothers, launching their "mythic

66. Vassiliki Betty Smocovitis, "I[sadore] Michael Lerner," in *New Dictionary of Scientific Biography*, ed. Noretta Koertge, vol. 4 (New York: Charles Scribner's Sons, 2007), 274–78.

67. Smocovitis, "G. Ledyard Stebbins" (ref. 33); Smocovitis, "Dobzhansky" (ref. 33).

68. Theodosius Dobzhansky, *Genetics and the Origin of Species* (New York: Columbia University Press, 1937).

69. Goldschmidt had arrived at Berkeley earlier in 1936 but did not have a formal appointment until three years later.

70. Ernest Brown Babcock and Richard Goldschmidt, "A Mechanized Exhibit of Human Heredity," *Journal of Heredity* 30 (1939): 235–36.

collaboration" to understand plant evolution on the Stanford campus.[71] They joined researchers at the California Academy of Sciences, Mills College, the Placerville Forest Station, and other colleges and institutions in northern California in an informal group called "The Biosystematists." Founded in 1935 with the tentative name of "Linnaeus," or "Linnean Club," it was organized by Keck, Jens Clausen, Stebbins, and Babcock.[72] It met once a month, rotating among institutions. On occasion it drew invited speakers such as plant geneticist Edgar Anderson from the Missouri Botanical Garden and Carl Epling from the University of California at Los Angeles. At the heart of both the Biosystematists and Genetics Associated were Babcock's energizing spirit and ambitious attempt to work out evolution in one complex plant genus using a range of interdisciplinary approaches. Jens Clausen's description of Babcock's influence was not much of an exaggeration: "The Division of genetics has for many years been a mecca of evolutionists of many lands because of Babcock's work. . . . [i]n Europe, Babcock has for many years been recognized as being one of the foremost leaders in the world in the study of plant evolution and genetics."[73]

BABCOCK AND STEBBINS: THE RELATIVES OF *CREPIS* AND THE AMERICAN SPECIES OF *CREPIS* (1935–1941)

The collaboration between Babcock and his new junior geneticist, G. Ledyard Stebbins, was to prove pivotal to the *Crepis* research program and, indeed, to sorting through complex evolutionary mechanisms in the plant world that had

71. For reference to the Carnegie Brothers see Jens Clausen to W. H. Camp, 28 Feb 1942, CP, Folder C. See Smocovitis, "Botany and the Evolutionary Synthesis" (ref. 29) for a description of the "mythic collaboration," and see also Smocovitis, "Discipling Botany" (ref. 29); Patricia Craig, *Centennial History of the Carnegie Institution of Washington: Volume IV: The Department of Plant Biology* (Cambridge: Cambridge University Press, 2005).

72. Jens Clausen to E. B. Babcock, 23 Sep 1935; E. B. Babcock to Jens Clausen, 24 Sep 1935; Jens Clausen to E. B. Babcock 25 Sep 1935, all in CP, Folder Babcock (ref. 49). It appears that the name Linnaeus Club was used initially. See Jens Clausen to G. Ledyard Stebbins, 9 Jan 1938, CP, Folder G. Ledyard Stebbins Jr. The history of the Biosystematists is recounted in Lincoln Constance, transcription of interview by Ann Lage, "Versatile Berkeley Botanist: Plant Taxonomy and University Governance," 1986, on 95–97, TBL. I discuss the Biosystematists at greater length and include the membership list and a 1944 group photograph in Smocovitis, "G. Ledyard Stebbins and the Evolutionary Synthesis" (ref. 33). See also Hagen, "Experimentalists" (ref. 29). For a history of the Biosystematists see W. Z. Lidicker Jr., "An Essay on the History of the Biosystematists of the San Francisco Bay Area," in *Cultures and Institutions of Natural History and Philosophy of Science: Essays in the History and Philosophy of Science*, ed. M. T. Ghiselin and A. E. Leviton (San Francisco, CA: California Academy of Sciences (2000): 315–27.

73. Jens Clausen to Stuart Daggett, 30 May 1949, CP, Folder E. B. Babcock.

long bedeviled evolutionists and botanists going back to Darwin and Mendel.[74] At the heart of the problem were the complex phenomena later recognized as polyploidy (the doubling or multiplication of chromosome sets), apomixis (a kind of asexual reproduction in which the egg cell develops independently without fertilization), and hybridization. Evolutionists were interested not only in the specific mechanisms at play in each of these phenomena, but also in their interactions, especially alongside particular kinds of geographic distribution patterns in members of some groups of plants that defied easy classification. The Compositae were especially problematic. By 1935 much was known about polyploidy, its origins and prevalence, but its role in speciation, and the extent to which autopolyploids (those having multiples of homologous chromosomes) and allopolyploids (those having multiple sets of chromosomes from different species or genera) or even mixtures between the two contributed to evolutionary processes, was being actively questioned. What role hybridization played alongside polyploidy was likewise debated, and because hybrids were usually infertile and relied on asexual means of reproduction, apomixis was also considered. It was difficult to sort out precisely how any of these phenomena operated in the plant world, because they appeared to be so closely linked, if not in fact interdependent. To discerning systematists, moreover, particular patterns in genetic systems seemed correlated with particular geographic patterns observed in some groups. Sorting through the genetical process and the geographic patterns, by collecting and correlating both morphologic and cytologic data, was therefore the critical part of any project to determine evolution in any member of such a complex group.

By 1935 enough data on *Crepis* had been compiled to make for a complicated story. Research from the *Crepis* program had shown that species endemic to North America appeared to have a different pattern of genetic relationship than the Old World species, which were diploids with $n = 3, 4, 5$, and 6 pairs of chromosomes. Hybrids between these Old World forms were highly sterile with abnormal chromosome behavior. In contrast, the New World forms had a much higher chromosome number of 11, and hybridization was widespread. Babcock postulated that the New World forms with $n = 11$ were most likely allopolyploids

74. For a discussion of Darwin's botany in *On the Origin of Species* see Vassiliki Betty Smocovitis, "Darwin's Botany in *On the Origin of Species*," in *The Cambridge Companion to The "Origin of Species*," ed. Michael Ruse and Robert J. Richards (Cambridge: Cambridge University Press, 2008), 216–36; David Kohn, *Nature's Garden; An Evolutionary Adventure* (Bronx: New York Botanical Garden Press, 2008); Peter Ayres, *The Aliveness of Plants: The Darwins at the Dawn of Plant Science* (London: Pickering and Chatto, 2008).

of the Old World type of *Crepis* with n = 4 and some other undetermined Old World *Crepis* species.

From their distribution too, Babcock realized that the New World forms fell into two major groups. One group was found in the Midwest or in the plains west of the Missouri River as far as the eastern slope of the Sierra Nevada, and preferred watery environments. This group always consisted of diploids with 22 chromosomes. The other, more interesting group was found primarily along mountain slopes throughout the West from Colorado all the way to California and characterized by chromosome counts of 22 and 44. Morphological characters in this second group, moreover, seemed to blend or intergrade between the 22- and 44- chromosome types. Since many of these apparently intergrade forms showed aborted anthers and malformed pollen grains, Babcock suspected that this second group was strongly apomictic, meaning that it engaged in a form of asexual reproduction.

When Stebbins joined the *Crepis* project his initial responsibilities were to perform chromosome counts and work out the taxonomy of some of the nearest relatives of the genus in the tribe Cichorieae (the chicory tribe). But while carrying out the routine chore of chromosome counts, he became interested in Babcock's observations on the New World species of *Crepis*. These New World species reminded him of some of the relationship patterns that he had seen in genera he was familiar with, such as *Antennaria* (commonly known as pussyfoots) and *Paeonia* (the peonies).[75] But the *Antennaria* project, which he had worked on at Harvard while a graduate student, had shed only limited light on plant evolution: in his research on it Stebbins had found natural hybrids between two of the 28-chromosome forms of *Antennaria, A. plantaginifola* and *A. neglecta*, but they showed no evidence of apomixis and appeared to be ordinary, partially sterile hybrids. Even the hexaploid *A. parlinii* from northern Virginia showed no sign of apomixis. Stebbins therefore failed to find any examples in *Antennaria* that demonstrated a relationship between hybridization and apomixis to explore further.

His research on *Paeonia,* from his years at Colgate University, proved to be more helpful to understanding *Crepis* because it had a distribution pattern very similar to *Crepis*'s. Most of the hybrids he and his former collaborator

75. G. Ledyard Stebbins, Jr., "Cytology of *Antennaria* II. Parthenogenetic Species," *Botanical Gazette* 94 (1931): 322–45; G. Ledyard Stebbins, Jr., "Notes on the Systematic Relationships of the Old World Species of Some Horticultural Forms of *Paeonia*," *University of California Publications in Botany* 19 (Berkeley: University of California Press, 1939).

Percy Saunders had examined were diploids that were stable, easily recognized, well-circumscribed species separated by reproductive isolation barriers based on chromosomal differences. Some of the peonies, however, were tetraploids that seemed to blend or intergrade into each other. Each of the tetraploids appeared to have some different characteristics, and species lines between them were difficult to determine. When Stebbins and Saunders studied their distribution, they noticed that those tetraploids from the Mediterranean resembled very closely the diploid species of the Mediterranean *P. corallina* group. These tetraploids in turn seemed to grade continuously with another diploid, the *P. officinalis* group. Some of the more extreme *officinalis* tetraploids then resembled the *P. anomala* group, which was endemic to central and eastern Asia.[76]

When Stebbins joined the *Crepis* team and became familiar with Babcock's data on the North American species, he suspected that the explanation for the distribution of both *Paeonia* and *Crepis* was related in some way.[77] Excited at the prospect of finally resolving the distribution problem, Stebbins asked Babcock's permission to work alongside him on the North American species of *Crepis.* Babcock agreed, and after the spring of 1936 Stebbins divided his research time between the two projects.

Stebbins made two field trips to collect *Crepis.* On the first of these he accompanied Babcock to Oregon and northeastern California; on the second he accompanied James Jenkins to the same places and into western Nevada. After specimens were collected, chromosome numbers were determined and identification between the tetraploids and the diploids was made using differences in stomatal size and regularity of pollen grains. Once ploidy was determined, comparisons were made with previously collected herbarium specimens. Borrowing from the statistical techniques developed by the botanist Edgar Anderson for *Iris*, Stebbins also performed an analysis of variation between populations of *Crepis*.[78] Levels of variation were therefore compared among (and within) the diploids and polyploid forms. When all distribution and variation analyses were performed, using both living and herbarium specimens, a picture of the relationship among polyploidy, hybridization, and apomixis finally emerged. The results of this extensive study were finally published in 1938

76. Stebbins, "Notes" (ref. 75).

77. G. Ledyard Stebbins, interview by author, Jan 1987.

78. Edgar Anderson, "The Species Problem in *Iris*," *Annals of the Missouri Botanical Garden* 23 (1936): 457–509.

in a monograph entitled *The American Species of Crepis: Their Interrelationships and Distribution as Affected by Polyploidy and Apomixis*.[79]

The evidence overwhelmingly supported the complex nature of auto- and allopolyploidy. To describe this pattern of relationships that was the result of apomixis, hybridization, and polyploidy in the North American species, Babcock and Stebbins invented the novel concept of the agamic or polyploid complex. For both scientists, it was their claim to fame.

The *American Species of Crepis* and the Invention of the Polyploid Complex: Discussion

The lines of evidence and forms of reasoning used to understand the evolution of the American species that gave rise to the concept of the polyploid complex were largely indirect and complex in themselves. On the basis of the type of evolution that had taken place, Stebbins and Babcock classified the American species of *Crepis* into two groups. The first of these was made of the species *C. runcinata*, a sexual species that had not undergone chromosomal change since its inception from a hybrid between a 4-paired and 7-paired species. Evolution in this group appeared to be ordinary; it was the result of gene mutation and natural selection in response to environmental conditions. It was clear that *C. runcinata* was what German evolutionist Bernhard Rensch had in 1929 designated as a *Rassenkreis* or a polytypic species (meaning it was a proper species with a variety of forms).[80]

The second group was comprised of the nine remaining species, which were the products of different evolutionary processes involving polyploidy, apomixis, and hybridization. The sexual forms of these species were distinct from each other morphologically, were geographically restricted, and were genetically isolated from each other. Diploid hybrids between these groups did not exist, but polyploid forms were rampant. As Babcock and Stebbins described them, these polyploids were "either identical with one or other of the diploid forms except for size differences and different ecological preferences, or else combine[d] the characteristics of these forms."[81] These polyploids therefore appeared to intergrade

79. Ernest Brown Babcock and G. Ledyard Stebbins Jr., *The American Species of Crepis: Their Interrelationships and Distribution as Affected by Polyploidy and Apomixis* (Washington, DC: Carnegie Institution of Washington, publ. no. 504, 1938).

80. Bernhard Rensch, *Das Prinzip geographischer Rassenkreise und das Problem der Artbildung* (Berlin: Gebr. Borntraeger, 1929).

81. Babcock and Stebbins, *American Species* (ref. 79), 45.

with the diploids. With this in mind Babcock and Stebbins concluded "that divergent evolution has been at a standstill in these polyploids, and that all evolutionary changes within them have been through the activity of [polyploidy, apomixis and hybridization]."[82]

The morphological changes observed in this second group fell roughly into three main categories: those showing an increase in size (or "gigas" characteristics as a result of polyploidy); those showing the recombination of diploid characters (as a result of hybridization); and those showing the formation of microspecies (or species separated from other species based on minute differences). These apomicts demonstrated distinct variation patterns and appeared to center closely on a similar diploid form. Stebbins and Babcock named such a distribution consisting of diploids surrounded by polyploids an agamic complex. Such an agamic complex showed

> a marked concentration of variability at or near centers of distribution of the diploid sexual forms, and a progressive 'thinning out' of the biotypes at greater and greater distances from these centers so that the number of forms in any one locality becomes fewer and fewer, and they become more and more distinct from one another.[83]

The formation of such an agamic complex was the result of the hybridization of sexual forms, which produced polyploids, which in turn became apomictic as the result of unbalanced chromosomes numbers. Since many forms were facultative apomicts, moreover, Babcock and Stebbins suggested that the onset of apomixis was probably a gradual process. Apomicts most removed from their center of distribution were most likely those selected by environmental conditions. At the centers of origin (near the sexual diploids) apomicts were considered "beginners," the fate of most of which was "failure and oblivion," while at remote distances from centers of origin the apomicts were "veterans."[84]

To determine the ecologic advantages conferred on species demonstrating polyploidy, hybridization, and apomixis, Babcock and Stebbins compared the distribution of their "agamic complex" to their diploid sexual relative *C. runcinata. C. runcinata* showed a wider range of distribution than all the polyploid species together, and equal tolerance to extremes in temperature. If this were

82. Ibid., 45.
83. Ibid., 49.
84. Ibid., 50.

the norm, then Babcock and Stebbins were left to explain the nature of the advantage that polyploidy, apomixis, and hybridization conferred. They knew from other studies that hybridization resulted in vigorous hybrids. This was clearly the case with Canadian geneticist Leonard Huskins's well-known example of *Spartina townsendii,* in which newer polyploid forms had effectively spread at the expense of its diploid progenitor.[85] Polyploidy also seemed to produce new forms at a much quicker rate than ordinary genetical processes. Thus, Babcock and Stebbins suggested that polyploidy could confer a selective advantage in rapidly changing environments, where reproductive speed and vigor would be important. This explanation also could account for the rapid rise and spread of certain groups like the angiosperms (or the flowering plants) after disturbances such as the last ice age. Polyploidy could therefore be thought of as "a 'short-cut' by which a species or genus may adapt itself to a rapidly changing environment."[86]

In the case of *Crepis*, however, the polyploidy picture was more complicated since there appeared to be distinct differences between the autopolyploids and the allopolyploids. In *Crepis*, autopolyploidy, the mere doubling of the chromosome sets, produced only quantitative morphological differences such as increase in size and number of floral parts. The majority of novel divergent morphological types were therefore allo- rather than autopolyploid in origin. Autopolyploids in *Crepis* also did not show wider ranges of distribution than the allopolyploids, and autopolyploid distribution did not differ as much as expected from the diploids. Evidently, it was in the allopolyploids that new combinations of characters and new distribution in *Crepis* could be seen.

Since many plant groups demonstrated similar patterns of relationships as a result of apomixis, polyploidy, and hybridization, Babcock and Stebbins proposed an official systematic recognition of their existence. They therefore set forth the following definition:

> Any group of this sort may aptly be termed a *heteroploid* complex. A heteroploid complex may be defined as: *a group of species, containing forms with different chromosome numbers, of which those with the lowest number (i.e., the diploids) are more or less distinct from one another morphologically, and are usually isolated from one another by sterility barriers, but in which some of the aneuploid or polyploid types are intermediate between the diploids or show different recombinations of their characteristics.* In other words a heteroploid complex consists of three cytological and

85. C. Leonard Huskins, "The Origin of *Spartina Townsendii*," *Genetica* 12 (1931): 531–38.
86. Babcock and Stebbins, *American Species* (ref. 79), 52.

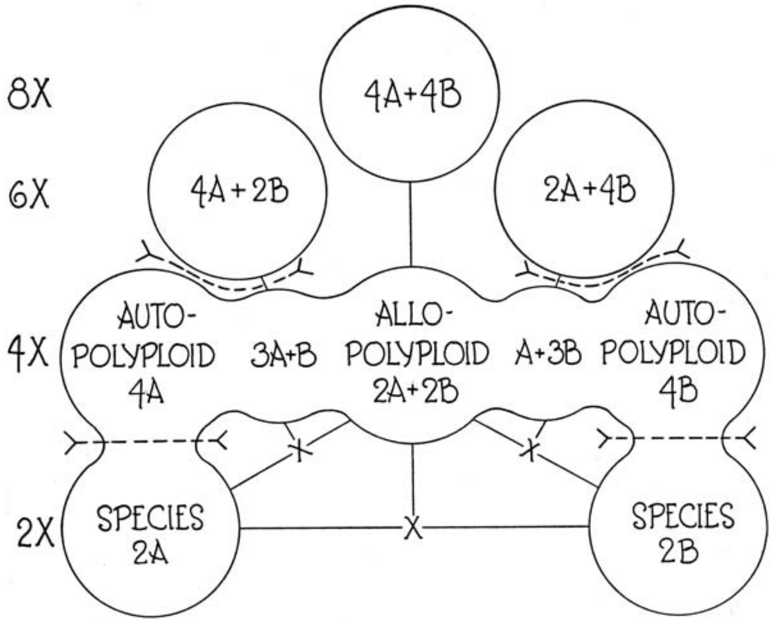

FIG. 4 Sexual Polyploid Complex. Hypothetical diagram illustrating a sexual polyploidy complex. Babcock and Stebbins, *American Species of Crepis* (ref. 79), 56.

morphological types, diploids, autopolyploids, and allopolyploids, the latter passing into each other by a series on intergrades.[87]

Heteroploid complexes were of three types: euploid (which were multiples of one basic number), polyploids, and aneuploids (which possessed unbalanced numbers of chromosomes). Of the three, polyploid complexes were the most common and were primarily of two types: sexual polyploid complexes and agamic heteroploid complexes. Agamic heteroploid complexes or agamic complexes were those groups in which propagation of the polyploid derivatives was through vegetative or asexual means. Sexual polyploid complexes were the most common in plants, but agamic complexes characterized taxonomically difficult groups like *Rubus, Rosa, Antennaria, Taraxacum,* and *Hieracium.* To visualize polyploid complexes Babcock and Stebbins drew the following two (hypothetical) diagrams. (Figs. 4 and 5) Unlike the conventional evolutionary trees depicting phylogenetic patterns, the unusual diagrams attempted to represent the complex patterns often seen in the plant world.

87. Ibid., 55.

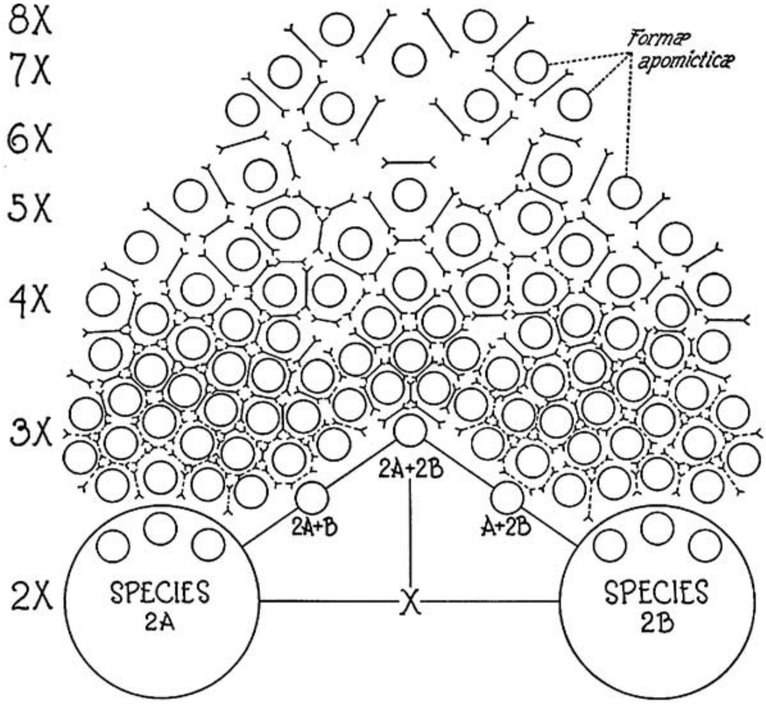

FIG. 5 Agamic Complex. Hypothetical diagram illustrating an agamic complex. Babcock and Stebbins, *American Species of Crepis* (ref. 79), 57.

In these diagrams the vertical axis represented the degree of variation as a result of polyploidy, and the horizontal axis represented genic differences. Genetic isolation was depicted by solid lines while broken lines indicated incomplete isolation. In Fig. 4, the sexual polyploid complex, the simplest instance was chosen, that of two existing diploids. In most groups (including *Crepis*) where several or more diploid groups were possible, the diagram would have to be perceived in three dimensions with the diploids forming the bases of a complex of polyploids on top. In Fig. 5, polyploids and aneuploids (those that lie between the vertical rows) were shown in relation to the diploids. Here the forms of polyploids and aneuploids were more numerous, and separated from each other depending on the degree of apomixis.

The evolutionary effects of heteroploid complexes became apparent when heteroploid-complexed species of *Crepis* were compared to the *Rassenkreis, C. runcinata.* Babcock and Stebbins realized that only one member of a *Rassenkreis* could be found within an ecological habitat, whereas two or more members of a heteroploid complex could be found in the same habitat since agamic members were reproductively isolated from each other. The nature of variation also differed between the members of a *Rassenkreis* and members of a heteroploid complex. While variations within a *Rassenkreis* were correlated with environmental conditions, heteroploid complexes were not necessarily correlated with environmental parameters.[88]

With this understanding, Babcock and Stebbins came to the conclusion that polymorphism was much more common in species with heteroploid complexes than in the *Rassenkreis*, and that the distribution of this variation differed. In a *Rassenkreis* the most extreme morphological types were seen at the periphery or geographic boundary of species ranges (in response to selection). The most extreme morphological types in the agamic complex, however, were seen at the center of the range of distribution centering on the diploid progenitors. In an agamic complex, forms that had arisen through polyploidy and hybridization and were adapted to environmental conditions were found at the extreme ends of the environment. These "highly selected" forms occupied the "isolated outposts" of species ranges and consisted of morphological blends. The principal effects of polyploidy were to increase the polymorphism of the group and to spread intermediate or "hybrid" types as well as "gigas" types morphologically similar to diploids over a large territory and in diverse habitats. Heteroploid complexes, in turn, were a group where the ordinary hybrid types had become the most common or dominant representatives. Viewed this way, they concluded, "the taxonomic diversity of these complexes becomes comprehensible, even though their classification according to the accepted methods still presents great difficulties."[89]

The role of apomixis when accompanied by hybridization and polyploidy was through its "rapid production and 'fixing'" of new variants in certain parts of the range of the group, as well as limiting variability in other parts of the range. Agamic complexes in locations adjacent to their distributional centers were better suited to taking advantage of changing conditions than sexual heteroploid complexes. Babcock and Stebbins wrote that this is "strikingly manifest

88. Babcock and Stebbins wrote: "In heteroploid complexes variation in the morphology and structure of the floral parts, i.e., the 'fundamental character' of the taxonomist, is much greater than it is in the *Rassenkreis.* A comparison between the type of variation found within the *Rassenkreis* of *C. runcinata* and that of the agamic complex comprising the nine other species will emphasize this point. The variations within *C. runcinata* involve chiefly the shape of the leaves, the stature of the plant, the degree of glandulosity, etc., while such characteristics as the nature of the inflorescence, the number of florets per involucre, and the color, shape, and ribbing of the achenes are relatively constant. The agamic complex, on the other hand, shows, in addition to the type of variation characteristic of *C. runcinata* extreme polymorphism in the characters of the flowers and fruits just mentioned . . . [t]his is due to the very different ancestry of its various diploid members." Babcock and Stebbins, *American Species* (ref. 79), 60.

89. Ibid., 61.

in the 'weedy' tendency of many apomicts of *Taraxacum, Hieracium,* and *Antennaria*."[90] But such agamic complexes with limited variation at the periphery of the range were also considered "closed systems" whose fate was "bound up in the fate of its sexual members." Such agamic complexes would "give rise to nothing new."[91]

If sexual members were to maintain an extensive range, furthermore, the opportunity for new apomicts would arise and the complex would maintain its "youth" and "aggressiveness"; but if the sexual forms became more isolated geographically, new apomicts would not arise as often and the species would become "senescent." If apomictic groups were to become separated geographically from the sexual ancestors, they would become "relict types" and would demonstrate little aggressiveness. The isolation of a sexual part of the population, however, would lead to constancy and conservatism in this population. The "ultimate fate" of an agamic complex in which the sexual ancestors became restricted or extinct was to continue to exist—but only so long as the conditions that existed during its formation continued to prevail. Unable to meet the environmental changes, the group would become more restricted in range and would eventually die out.[92]

With this understanding of the structure of heteroploid complexes and the evolutionary effects of polyploidy, hybridization, and apomixis, Babcock and Stebbins attempted to devise a systematic treatment for members of an agamic complex. Species definitions based on homoploid sexual groups could obviously not apply to members of an agamic complex. Instead, new methods had to be devised to identify its members; Babcock and Stebbins, moreover, also stressed "the necessity of studying the whole of an agamic complex before a satisfactory treatment" was possible, combining the tools of cytogenetics and morphology with a detailed study of geographic distribution.[93] To deal with the ubiquitous intergrading apomictic forms, Babcock and Stebbins drew on a 1926 precedent established by Swedish genecologist Göte Turesson and designated these forms "*apm*" or *formae apomicticae.*[94] This was a utilitarian category

90. Ibid.

91. Ibid.

92. Ibid.

93. Ibid., 69.

94. Jens Clausen had introduced Babcock and Stebbins to Turesson's work and made the suggestion that they employ the designation of "*formae apomicticae*." See Jens Clausen to G. Ledyard Stebbins Jr., 6 Sep 1936, CP (ref. 72). Clausen had also urged them to be cautious with the term "heteroploid" and pointed them to the 1916 work by H. Winkler on the chromosomes. H. Winkler,

that did not recognize the forms as proper taxonomic entities and avoided traditional discussions about the proper status of varieties or other subspecific categories.

Taken as a whole, the 1938 monograph by Babcock and Stebbins was a detailed explanation of the kinds of evolutionary processes that had given rise to the American species of *Crepis*. It was an impressive exercise in the philosophy of science in general, and the philosophy of evolutionary science in particular, and a synthesis of the knowledge that had accumulated on the *Crepis* research to date. Noteworthy in its demonstration of diverse methodologies, from statistical analysis to the novel application of cytological and genetical techniques, to traditional biogeographical mapping and herbarium taxonomy, and very much a representative of the "new systematics" just beginning to sweep biological circles, this kind of interdisciplinary approach offered new understanding of problematic or difficult groups.[95] Its ultimate use, therefore, was in sorting what appeared to be the chaotic patterns of varied forms into an explanatory scheme that could then be adapted for utilitarian ends, namely the designing of a taxonomic scheme grounded in phylogeny.

Clearly, the monograph made an important contribution to plant systematics; but it also had a much wider audience outside of botanical circles. The fact that evolutionary processes in plants were so vastly different than those seen in mammals, birds, and insects made the data of great interest to those seeking a general theory of evolution. For that reason, zoologists like Dobzhansky began to turn to plant geneticists, systematists, and biogeographers. Beginning in the late 1930s, Dobzhansky spent more and more time in northern California, interacting with plant evolutionists such as Stebbins and Clausen, while at the same time engaging in his own detailed research program into the evolutionary genetics of *Drosophila pseudoobscura*.[96] Dobzhansky's research program as a whole, in fact, bore notable parallels to the *Crepis* program; both sought to integrate genetical, cytological, morphological, and biogeographical information in order to understand the genetic basis of evolutionary change. The influence of plant evolution on Dobzhansky's formulation of the synthetic theory was apparent by 1941, when the *Crepis* study and other work by

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"Uber die experimentelle Erzeugeung von Pflanzen mit abweichenden Chromosomenzahlen," *Zeitschrift Botanische* 8 (1916): 417–531; Jens Clausen to G. Ledyard Stebbins, Jr., 30 Nov 1937, CP (ref. 72).

95. Huxley, *New Systematics* (ref. 32).

96. See Lewontin et al., *Dobzhansky's Genetics* (ref. 7).

botanists was incorporated into the revised edition of *Genetics and the Origin of Species.*[97]

In 1943 Julian Huxley, the editor of *The New Systematics,* appreciated the importance of the *Crepis* project and the polyploid complex so much that he included it in his influential book, *Evolution: The Modern Synthesis*.[98] More than any other, this book heralded the new synthesis of evolution, which sought to integrate Darwinian selection theory with Mendelian genetics. It was a fitting inclusion, especially since Mendel's confusion over *Hieracium* could finally be resolved, but Huxley also erroneously accredited the polyploid complex to the genus as a whole. To Babcock's consternation, Huxley's mistake revealed that he had confused the American species of *Crepis*, which demonstrated such complex patterns, with the genus as a whole, while it was becoming apparent to Babcock in the early 1940s that polyploid complexes were not in fact characteristic of the whole genus.[99] Nonetheless, Babcock was pleased to see the *Crepis* project incorporated into the new literature of the "modern synthesis," though he included a carefully worded correction to Huxley in 1947, when addressing evolution in the genus as whole.

The monograph on the American species of *Crepis* was by all standards a success. It received strong reviews in the press: Åke Gustafsson proclaimed "[t]he most important work on the formation of species has seen the light of day."[100] And it was praised in private: in one report, Jens Clausen wrote, "I consider Babcock and Stebbins' new book on the American Crepis, now in print, the best systematic-evolutionary treatment of any group of agamic species, representing an entirely new departure in the treatment of such species."[101] Of the entire *Crepis* program he also noted: "with many others I consider Crepis

97. Dobzhansky's preferred field site in the early to mid-1940s was Mather, California, the base camp for the Carnegie team and the field site used by Ledyard Stebbins. Some of his experimental materials, e.g., bottle preparations for *Drosophila*, were prepared at Berkeley; see Jens Clausen to E. B. Babcock, 5 Jun 1945, CP, Folder, E. B. Babcock. For more on Dobzhansky and plant evolution see Smocovitis, "Dobzhansky" (ref. 33).

98. Julian Huxley, *Evolution: The Modern Synthesis* (London: Allen and Unwin, 1943). Others who included extensive reference to Babcock's *Crepis* in their books were Richard Goldschmidt, who gave three pages to it in *The Material Basis for Evolution* (New Haven, CT: Yale University Press, 1940), and Lester W. Sharp, who devoted four paragraphs to Babcock's work and reproduced two of his diagrams in his brief textbook *Fundamentals of Cytology* (New York: McGraw-Hill Co., 1943).

99. Babcock, *Genus Crepis* (ref. 8), 27.

100. Äke Gustafsson, *Apomixis in Higher Plants* (Lund, Sweden: C. W. K. Geerup: Ernest Brown, 1946–1947), 6.

101. Jens Clausen to E. B. Babcock, 30 Jul 1938, CP (ref. 2).

next to Drosophila in evolutionary importance among American research, but Crepis has the wider of the systematic appeal of the two."[102]

COMING TO FRUITION: *THE GENUS CREPIS* (1947)

After the success of the North American *Crepis* project and the elucidation of the polyploid complex, Babcock turned his attention to the completion of his monograph on the evolution of the genus. Much work remained to be done, and rapidly, if he were to complete a comprehensive monograph on the entire genus before his retirement. Babcock's three-year Rockefeller grant was running out, and funds were needed to sustain research and to employ his assistants. In 1937 Babcock had been able to hire Jenkins as an instructor in the division, but funds were still needed to sustain Stebbins, with whom he had had an especially productive collaboration and who made an "excellent impression."[103] In 1938 Babcock applied to the Rockefeller Foundation to extend his grant for one more year, arguing that the time was needed for Stebbins to complete his cytological studies. Research would continue as planned, but Babcock now intended to do more work on the developmental morphology of the genus.[104] The request was for salary (increased to $3,500) and $500 for incidental expenses. It was endorsed by the Harvard geneticist W. E. Castle, who had worked closely with Stebbins and was a frequent visitor to the lab.

Babcock was disheartened to learn, however, that his application was almost immediately rejected. The terse letter he received from Frank Blair Hanson stated only that "funds had been committed for the remainder of this calendar year and ear-marked for the year 1939."[105] Privately, however, Hanson had a somewhat different view of the "plant genetics" project at the University of California:

> This is not an exciting area of investigation, in which new or revolutionary principles will be discovered, but is rather one where long-sustained and patient application of known principles and methods of cytology and genetics is used to solve important problems of phylogeny and evolution.

102. Ibid.

103. E. B. Babcock, 13–23 Apr 1938, RG, Box 12, Folder 176.

104. "Progress of the Plans for Completion of an Evolutionary Study of the Cichorieae, 24 May 1938," RG, ibid.

105. Frank Blair Hanson to E. B. Babcock, 23 May 1938, RG, ibid.

> Such studies will eventually find their proper place in the completion of the evolutionary picture, and in any large program of research in cytogenetics deserve a minor share of financial support. However, in a period of RF retrenchment this project is representative of that portion of the RF program in experimental biology which can be eliminated with least harm to a developing science.[106]

It was indeed a period of retrenchment, but also one that was seeing a shift in support for newer sciences such as biochemistry and "molecular biology" (the celebrated term coined by Rockefeller official Warren Weaver). Studies of systematics, phylogenies, and evolutionary reconstruction, no matter how inventive they had initially appeared, were no longer slated for support.[107] The peak period of interest in the project had waned, which was all the more reason for Babcock to step up research to complete his monograph. He was lucky; in 1938 he obtained modest funds from the American Philosophical Society to continue the project and retain Stebbins for the year. Stebbins was eventually hired as assistant professor in the division the following year.[108] Their collaboration lasted for another six years, leading to a series of articles on the genetics of the evolutionary process in the genus, and to another monograph on the Asiatic genus *Youngia,* a closely related genus.[109]

"New Light on Evolution from Research on the Genus *Crepis*": Discussion

By the early 1940s Babcock had changed his earlier position on the genetic nature of evolutionary processes, not only because of the data he had accumulated

106. "University of California–Plant Genetics," RG, ibid.

107. For more on Rockefeller Foundation funding see Robert E. Kohler, *Partners in Science: Foundations and Natural Scientists, 1900–1945* (Chicago: University of Chicago Press, 1991); Robert E. Kohler, "The Management of Science: The Experience of Warren Weaver and the Rockefeller Foundation Programme in Molecular Biology," *Minerva* 14 (1976): 279–306; Pnina Abir-Am, "The Discourse on Physical Power and Biological Knowledge in the 1930s: A Reappraisal of the Rockefeller Foundation's 'Policy' in Molecular Biology," *Social Studies of Science* 12 (1982): 341–82; Lily E. Kay, *The Molecular Vision of Life: Caltech, the Rockefeller Foundation and the Rise of the New Biology* (Oxford: Oxford University Press, 1993). Learning that Weaver would be visiting the campus, Babcock made an attempt to arrange an appointment. Weaver's secretary wrote back with an officious note stating that "He [Weaver] expects to spend most of Tuesday morning with Professor [Ernest O.] Lawrence. Since he hopes to see several persons while he is at the University it is hard for him to arrange appointments in advance, and he will therefore expect to get in touch with you from Professor Lawrence's office some time Tuesday morning." Secretary to Mr. Weaver to E. B. Babcock, 9 Jan 1939, RG (ref. 103).

108. The sum requested from APS's Penrose Fund was $400. E. B. Babcock to Jens Clausen, 25 Jul 1938, CP, (ref. 2). It is not clear how Babcock paid Stebbins's salary for the year.

109. Ernest Brown Babcock and G. Ledyard Stebbins Jr., *The Genus Youngia* (Washington, DC: Carnegie Institution of Washington, publ. no. 484, 1937).

on *Crepis* but also due to insights coming from workers such as Dobzhansky and the Carnegie team of Clausen, Keck, and Hiesey. He was in especially close contact with Clausen and in 1940 accepted an appointment as research associate at the Carnegie Institution of Washington.[110] Opportunities arose to pull all the accumulated data together, and beginning in the early 1940s, he wrote a series of articles assessing evolution in the genus as a whole that reflected his mature views. It was an appreciably altered picture of general evolution compared to his earlier views. Four major processes could now be responsible for evolution in the genus: (1) structural transformation of the chromosomes; (2) interspecific hybridization; (3) gene mutation (also termed point mutation); (4) polyploidy and apomixis (discovered in the American species of *Crepis*). Gene mutation, of whose importance Babcock had in the 1930s been unconvinced, he now conceded to be at least as important as structural transformation of the chromosomes in the evolution of this genus, while "[p]olyploidy and apomixis have played a very definite but relatively unimportant role in the evolution of *Crepis*."[111]

In 1944 Babcock delivered the prestigious Faculty Research Lecture at the University of California, which he revised for a prominent synthetic article in the *American Naturalist*, "New Light on Evolution from Research on the Genus *Crepis*."[112] In it Babcock laid out his understanding of evolution in the entire genus to date. His *Crepis* data confirmed the Darwinian tenet that evolution resulted from the slow, gradual operation of natural selection on small, heritable differences. He corrected the historical misperception introduced by de Vries that large-scale changes could lead to new species, and gently opposed a similar position "revived by one of our colleagues" that new species originated through some sort of "systemic mutations" due to alterations of chromosomes.[113]

110. E. B. Babcock to V. Bush, 27 Dec 1940, CP (ref. 2).

111. Ernest Brown Babcock, "Systematics, Cytogenetics, and Evolution in *Crepis," Botanical Review* 8 (1942): 139–90, on 185.

112. Ernest Brown Babcock, "New Light on Evolution from Research on the Genus *Crepis*," *American Naturalist* 73 (1944): 385–409.

113. Babcock was likely referring to the recent views of his zoology colleague Richard Goldschmidt, though he was not named in the text or cited at the end. In 1941 Babcock exchanged a series of letters with his Berkeley colleague, Richard B. Goldschmidt over which kind of genetic evolutionary process dominated in the genus. Babcock wrote to Goldschmidt that he took "serious exception" to Goldschmidt's "assumption that, in a given group of organisms—say Crepis—only *one* kind of genetic evolutionary process can be playing an important role." Babcock wrote: "I see no justification for your two *exclusive* alternatives: either neo-Darwinism or no neo-Darwinism. On the contrary," he continued, "I have always recognized that the evidence for Crepis indicates

Babcock based his views on the 113 species he had examined cytogenetically. They displayed a series of 12, 10, 8 or 6 chromosomes, (or n = 6, 5, 4 and 3 chromosomes), with some notable exceptions like the American species, which he now thought were special cases. Such a numerical pattern suggested the loss or addition of single chromosomes within such sets. Framing his paper with one dominant question—"[D]oes the origin of new species depend primarily upon such changes in chromosome number?"[114]—Babcock proceeded to organize the nearly thirty years of findings by numerous workers on the genus, first by sorting the species into sections so that all species within each subgroup were more closely related to each other than to members of other sections. To do this, he relied again on varied lines of evidence including standard morphological and anatomical data, along with the more novel cytological analysis, hybridization experiments, and consideration of geographic range.

Based on statistical analysis of trends in and between the sections he made two important observations. The first was a strong positive correlation between phylogenetic position and diminished chromosome numbers (e.g., sections I–V, with the most primitive species were n = 6, while sections XIX–XXVII with some of the more advanced species were n = 4 and n = 3). The second was a strong positive correlation between phylogenetic position and length of life of the individual plant. In other words, primitive groups tended to be perennials while the most advanced species tended to be annuals. To Babcock, the morphological, cytological, and physiological evidence pointed to a reduction in chromosome number and a shortening of the life cycle which accompanied morphological reduction and specialization of the forms.

Hybridization studies, in both the field and the laboratory, provided crucial evidence of the kinds of mechanisms of speciation in *Crepis.* For example, in one case, the existence of an interspecific lethal gene was detected that prevented hybridization, and in several artificial crosses between species of the same chromosome number, data were obtained showing that the two species differed in numerous minor gene differences affecting the size and shape of the various parts of the plant. From such data, Babcock inferred that "species

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that *both* gross structural changes and 'gene mutations' must be of importance in evolution and that natural selection must enter into the picture in connection with either or both types of genetic change." E. B. Babcock to Richard Goldschmidt, 23 Apr 1941, Richard Benedict Goldschmidt Papers, Box 1, Folder Miscellany-B, TBL. Goldschmidt's response has not been preserved but it is clear that the debate between the two continued. See ibid.

114. Babcock, "New Light" (ref. 112), 389.

diverged from a common ancestor through accumulation of minor gene mutations."[115] Another series of hybridization experiments between intersectional and intrasectional members of his classification scheme confirmed the scheme based on morphological data alone.

Two additional studies on the genus provided critical cytogenetical information. The first was the work of Russian cytogeneticist Helen Gerassimova, a co-worker of Michael Navashin's (and later his spouse). Through the use of x-ray irradiation of seeds, she generated a form of *Crepis tectorum* that resembled it morphologically, had the same chromosomal material, and was self-fertile, but could not breed back to the original *C. tectorum.* While possessing the same chromosome complement, the new plant possessed broken and exchanged pieces, in reciprocal translocation, of one pair of chromosomes. Sexually isolated from *C. tectorum*, the new plant received a new species designation that Gerassimova named *C. nova*.[116] Such a "mechanical" process, Babcock postulated, might have been responsible for the reduction from 4 to 3, or 5 to 4 chromosomes; as the name implied, furthermore, it was a kind of new species.

The second study was by his former star student and one of his international recruits from Egypt, Hassan Tobgy. Tobgy crossed two closely related species, *C. neglecta* (n = 4) with *C. fuliginosa* (n =3), and studied the behavior of the chromosomes in the sterile hybrids (n = 7).[117] Comparing them with the configurations at reduction division of *C. neglecta* and *C. fuliginosa*, and in particular their pairing patterns or configurations, Tobgy concluded that *fuliginosa* either had originated from *neglecta,* or the two had actually arisen from a shared ancestral form that was n = 4. The same kind of pattern, from a 5-chromosome to a 4-chromosome form, was observed by Marta Sherman Walters, another *Crepis* worker in Babcock's group in 1944.[118]

The evidence based on "comparative morphology, physiology, genetics, and cytogenetics," the fields or disciplines that Babcock understood to be relevant

115. Ibid., 395.

116. H. Gerassimova, "Chromosome Alterations as a Fact of Divergence of Forms, I. New Experimentally Produced Strains of *C. tectorum* which Are Physiologically Isolated from the Original Forms Owing to Reciprocal Translocations," *Comptes Rendues de l'Académie des Sciences de l' U.R.S.S.* 25 (1939): 148–54. Babcock readily accepted the new classification of the new species she proposed.

117. H. A. Tobgy, "A Cytological Study of *Crepis fuliginosa*, *C. neglecta*, and Their F_1 Hybrid, and Its Bearing on the Mechanism of Phylogenetic Reduction in Chromosome Number," *Journal of Genetics* 45 (1943): 67–111.

118. This had been part of her doctoral dissertation research. Babcock, "New Light" (ref. 112).

to his project, were consistent with the view that *Crepis* was monophyletic (that is, having one common ancestor).[119] This implied that the genus had a well-defined "center of origin," from which forms had adaptively radiated toward their worldwide distribution. The final part of Babcock's project was therefore to study the geographic distribution of the genus to determine possible migratory routes from a single center of origin. To do this, Babcock compared the geographic distribution of older and younger species in each of his sections. When he did this, it became apparent that a pattern was emerging consistent with the inference that the center of origin was north central Asia. This pattern was also consistent with an important and well-known principle of paleontology called Matthew's Principle, which stated that "in groups of related species living at a given time, the most primitive will be found farthest from the center of origin." Babcock thus noted "[t]he conformity with Matthew's Principle which we find in *Crepis* strengthens our assumption that central Asia is the center of origin in this genus."[120]

In some respects, this final portion of Babcock's project was the most path-breaking of all. Relying not just on traditional floristics and the biogeography of the genus, Babcock also employed data and principles from general paleontology to understand evolution in the genus. In the context of what began as a genetics research program, the use of biogeographical and paleontological data was unprecedented. Babcock drew heavily on paleobotany, and the area then known as ice age biology, to follow the migratory routes of the plant from its Asiatic source of origin. (Fig. 6) He also followed the plants up and down altitudinal gradients, and into low-lying marshes and deserts. At a time before the acceptance of continental drift, Babcock drew on the then-popular idea that a number of land bridges had served as terrestrial conduits along which plants like *Crepis* migrated to places such as Europe, North America, and Africa. His deductions, based on the distributional consideration of his sections, were confirmed by the presence of fossil seeds, some of which closely matched seeds of three existing species, one of which was a primitive "relic" species of the high Alps, while the other two were less primitive (but nonetheless not advanced) forms. Dating the various seeds along these distributional gradients, Babcock postulated that *Crepis* must have originated not later than the Miocene period. Although he acknowledged that his account of the evolutionary history of *Crepis*

119. Ibid., 399.

120. Ibid, 401. For more on Matthew's Principle see Ernest Brown Babcock, "Supplementary Notes on Crepis II. Phylogeny, Distribution and Matthew's Principle," *Evolution* 4 (1949): 374–76.

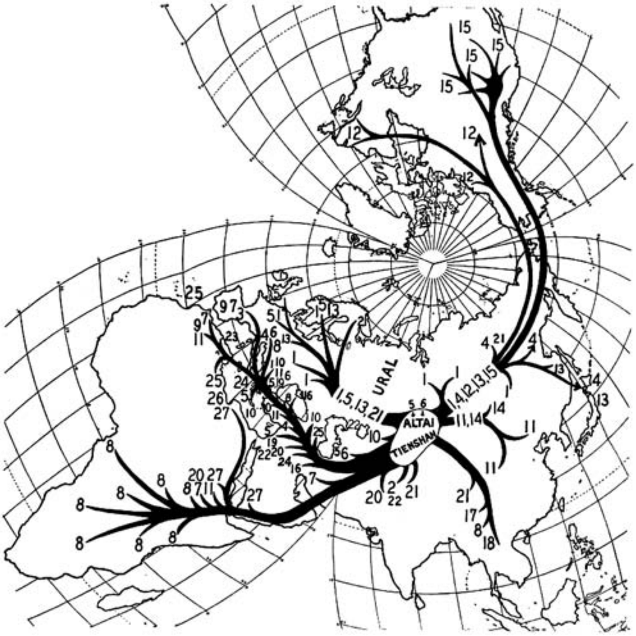

FIG. 6 Migratory Routes of *Crepis* form the assumed center of origin of Central Asia. Numbers designated sections from Babcock, *Genus Crepis* (ref. 8), 152.

was "hypothetical," Babcock took pains to point out that it was "consistent with the facts and accepted hypotheses of geology, paleontology and floristics."[121]

Babcock characterized the process of evolution in the genus as a whole in terms of three conditions and three vital processes. The first condition he denoted as "secular," by which he meant the amount of time it had taken for the complex genus to evolve; dating its origin and spread from the Miocene gave the genus "something like 20 to 30 million years" to evolve to its present state.[122]

121. Babcock, "New Light" (ref. 112), 403. To some extent the final part of the *Crepis* project mirrored an attempt made by botanist Carl Epling and Theodosius Dobzhansky to map the phylogenetic history against the geologic history of *Drosophila pseudoobscura.* In the latter case, the plant fossil record was used indirectly to infer the evolutionary dynamic of *Drosophila*. Epling's final portion of the Carnegie monograph, titled "The Historical Background," that they published together in 1944 met with questionable success. See Smocovitis, "Keeping Up with Dobzhansky" (ref. 33) for more on the controversial reception of the Dobzhansky and Epling collaboration on *D. pseudoobscura,* and especially the response to Epling's portion; and see Theodosius Dobzhansky and Carl Epling, "Contributions to the Genetics, Taxonomy, and Ecology of *Drosophila pseudoobscura* and Its Relatives" (Washington, DC: Carnegie Institution of Washington, publ. no. 554, 1944).

122. Ibid., 405.

Although many of the species were perennials, all produced new seed progeny each year, so Babcock estimated the number of generations since its radiation also at some twenty to thirty million, which increased the likelihood of new favorable types emerging. In the same span of time, Babcock noted, the earth itself had passed through three geological epochs and had entered a fourth; such a slow but profound series of changes would also force plants to adapt to new environments, or to migrate or face extinction.

The second condition played more directly on such environmental changes. Three in particular figured prominently in the evolution of this genus: first, the cooling and drying during the Miocene and Pliocene, which Babcock felt "induced" the southward trend in migration; second, the process of mountain building that included the Sino-Himalayan region, the Alps, the Pyrenees, and the Grand Atlas ranges, which opened up new migration routes for some species, while creating barriers for others; and finally, the effects of the Pleistocene glaciation event, especially the vacillations in moisture and cooling, which Babcock thought helped explain the fact that the Mediterranean had the highest concentration of younger species.[123]

Babcock's third condition was isolation, which he thought could potentially be accomplished in two ways: through migration, which could be either altitudinal or horizontal; or through genetical means, whereby mechanical changes in the chromosomes led to reductions in numbers (e.g., from 6 to 5, and from 4 to 3) and eventually to the creation of barriers in the production of fertile progeny. Such was the case with the *C. tectorum* studies by Gerassimova.

Babcock's first "vital process" accomplished the same thing as isolation in the first step in the process of speciation. This was the sexual isolation of different parts of the same population through some kind of internal mechanism that became more effective at dividing populations with time. His second vital process was that of differentiation between such isolated populations, which was due to gene mutations. Whether spatial or internal in nature, separation was enhanced by gene mutations, which had the potential to be able to create "endless changes in the form and function of the plant and its part," some of which, Babcock noted, might be nonadaptive in nature.[124] His third vital process was adaptation through gene mutation and natural selection. The adaptations Babcock had in mind for the genus included the change in type of root from a rhizomatous to a deep tap root, which enabled perennials to withstand xeric

123. Ibid., 406.
124. Ibid., 407.

(or dry) conditions; the reduction in the length of the life cycle, which conferred an advantage in xeric conditions; the increased durability of the seeds; and the increasing sophistication for their distribution especially by wind.

Since the most extreme adaptations were still connected through a long series of intermediate or more primitive species, and since hybridization experiments on interspecific hybrids showed they differed in a number of genes, the net result of Babcock's research led to the conclusion "that there is no reason to doubt and many reasons to believe that the basic cause of all this evolution through adaptation is gene mutation."[125] Babcock summarized his findings on *Crepis* that he later extended to his general view of plant evolution:

> We have found that the evolution of *Crepis* rests on three conditions, namely plenty of time; plenty of environmental changes with the passage of time; and isolation of populations through migration; and on three vital processes: (1) the creation of isolation through changes in chromosome numbers and associated genetic changes; (2) differentiation of species within the several chromosome number groups by means of gene mutations; (3) along with differentiation, adaptation through gene mutation and natural selection.[126]

And, finally answering his initial framing of whether chromosome change or gene mutation had been more important in this genus, Babcock concluded:

> We can state with assurance that changes in chromosome number, and the attendant changes in chromosome structure, have been important in creating isolation between groups of individuals within a species; and that these structural changes probably account for the arithmetical series of chromosome numbers found in many genera of animals and plants; but that they have not been important in creating the morphological and physiological differences between species. This differentiation process in the origin of species, we have found, is made possible by the accumulation of gene mutations occurring in already isolated groups or populations.
>
> These two conclusions are in general agreement with most other recent investigations in this field. They are diametrically opposed to the hypothesis of speciation by sudden, profound changes in species. At the same time they contribute to a still broader and firmer foundation for the neo-Darwinian theory of evolution.[127]

125. Ibid., 408.
126. Ibid., 409.
127. Ibid.

And contribute they did. The work on *Crepis* exemplified the kind of interdisciplinary and synthetic approach to evolution that integrated genetics, cytology, botany, biogeography, and systematics with paleontology; it contributed to, and reinforced, the growing consensus that natural selection acted on small, individual differences and that the tempo of evolution was slow and gradual. It also demonstrated exactly the kind of microevolutionary-macroevolutionary continuity that was increasingly part of the new or modern understanding of evolution gaining currency at the time, and in fact was at the vanguard of what was emerging as the "Modern Synthesis." The paper was a model of clarity and logic in presentation, concealing the indirect, or inferential, frequently convoluted, and varied means and methods that Babcock and his *Crepis* team had used to formulate a coherent view of evolution in the genus.

That complexity, and the very scaffolding for the interpretive picture Babcock had first unveiled in 1944, was finally revealed in the capstone publication of the *Crepis* research program, a two-volume monograph published in 1947, titled simply *The Genus Crepis*. (Fig. 7) In it, Babcock offered a rationale for his research program, beginning with a brief history of investigations in the genus, the general interpretive picture of evolution in the genus, and a detailed systematic treatment of it. Replete with the data of over a dozen co-workers, assistants, and students working for over thirty years, the monograph's two-page acknowledgment section detailed the names of hundreds of colleagues all over the world who had contributed to the project. It included copious tables, charts, maps, illustrations, the classification schemes, and taxonomic keys belonging to classical herbarium taxonomy, in addition to its analytical essays interpreting the data, and a substantive appendix on problems calling for further research. The first such comprehensive evolutionary study of an entire genus, Babcock drew on all the techniques and methods from all areas available to him at the time. Those techniques, particularly from cytology and genetics, were especially useful for determining phylogenetic relationships in conjunction with morphology and fossil history. While comparative morphology provided the primary basis for inter- and intrageneric classification in the Crepidinae (the tribe), Babcock noted that in *Crepis,* at least, the "evidence from comparative karyology, genetics, and cytogenetics has proved to be of the greatest value in determining phylogenetic relations and thus in approximating a truly natural classification."[128]

Finally, Babcock used the monograph to justify the support he had received from his institution. This was important, because resources had been expended

128. Babcock, *Genus Crepis* (ref. 8), 27.

FIG. 7 Frontispiece from *The Genus Crepis*. *Crepis sibirica*, on the left, is the most primitive and *C. suberostris,* on the right, is the most advanced species in the genus having 5 pairs of chromosomes. Chromosomes of each are depicted on top. All are on same scales. Babcock, *Genus Crepis* (ref. 8), frontispiece.

for a nonagricultural plant. On page one, he acknowledged his institution's generosity by writing, "[t]his continuous support of fundamental research on a group of noneconomic plants throughout a period of twenty-five years by an agricultural institution reveals a far-sighted policy on the part of the administration of the California Agricultural Experiment Station. It is the hope of the author that the results of these investigations, as summarized by this monograph, will be found to justify such a policy."[129] Although Babcock also quickly pointed out that some of the species were actually useful—some were consumed by livestock as wild foraging material, or by "country people" as salad greens; others served as ornamental plants. One species, known to be poisonous, held promise as a treatment for heart ailments, while yet another was a source of "crepin," a recently discovered chemical with potential antibiotic properties; and given the fact that antibiotics like penicillin had only just been mass marketed, this

129. Ibid., 1.

was an especially promising venue to pursue to justify work on the systematics of the genus. It was a familiar rhetoric used by botanists to justify sustained scientific interest in plants, but nonetheless could not mask what had become fundamentally an evolutionary inquiry divorced from traditional applications in agriculture and medicine. As one indicator of its systematic nature, the monograph was "dedicated as a memorial" to his old plant-loving friend, Harvey Monroe Hall, who had died unexpectedly in 1930 and thus had not witnessed the fruition of a research program he had helped to inspire.[130]

The book's appearance was timely. Babcock retired in the same year it was published, and along with the general acclaim and attention the monograph received, it garnered tributes and recognition for its author. In both reviews and private correspondence words such as "monumental," "crowning achievement," and "milestone" were used to describe the book.[131] It also enabled systematists to celebrate Babcock's work as representative of the new evolutionary and interdisciplinary approach to ordering the natural world. As his colleague at Stanford wrote Babcock upon reading only the draft version of the manuscript: "Your *Crepis* monograph shows that you are still in the forefront, and we greet you, therefore, not as the symbol of a past area, but as the standard bearer of the coming science of biosystematics."[132]

Despite Clausen's words of praise to the contrary, Babcock was no longer at the forefront; by 1947 he was rapidly becoming a symbol of a past era. Though his research program represented the new systematics and upheld the tenets of the modern synthesis of evolution, his own efforts at the new science called evolutionary biology were rapidly being overshadowed by younger researchers like George Ledyard Stebbins Jr., who in 1945 was described as the "young spark plug" in Babcock's department and full of "very stimulating ideas."[133] In 1947, it was Stebbins who delivered the Jesup Lectures at Columbia University, prompted by Dobzhansky's encouragement a few years before.[134] Those lectures, revised for publication, formed the backbone of Stebbins's 1950 book titled *Variation and Evolution in Plants.*[135]

130. Ibid., dedication page.

131. H. Spoehr to E. B. Babcock, 11 Sep 1947; CP; E. B. Babcock to Stuart Daggett 30 May 1949, both in CP (ref. 2). See also "Remarks by Roy E. Clausen at the Babcock Memorial Service," 19 Dec 1954, JAJ (ref. 3).

132. Jens Clausen to E. B. Babcock, 13 May 1946, CP (ref. 2).

133. Jens Clausen to Mogens Westergaard, 2 Sep 1945, CP, Folder Westergaard, Dr. Mogens.

134. See Smocovitis, "Dobzhansky" (ref. 33) for more details.

135. G. Ledyard Stebbins Jr., *Variation and Evolution in Plants* (New York: Columbia University Press, 1950).

Though Babcock had been as active as any of the figures associated with the creation of the new Society for the Study of Evolution (he was a founding member, signatory, and one of the three first vice-presidents), and had participated in community discussions pertaining to dominant themes in evolution, he was rapidly supplanted by his star protégé in the circle of "architects" of the "evolutionary synthesis."[136]

Initiatives were also underway locally at Berkeley that were rendering the *Crepis* research increasingly passé. Postwar developments there mirrored national shifts of interest in and support for the life sciences. The University of California's powerhouse President, Robert Gordon Sproul, did not favor the classical areas of the biological sciences; he instead slated newer areas connecting the biological sciences with the physical sciences, such as biochemistry, for support.[137] Although genetics remained a vital growth area, classical and evolutionary genetics were taking a back seat to newer areas such as physiological genetics, biochemical genetics, and human genetics, areas that were being increasingly shaped outside of Babcock's division. In 1947 for example, when drosophilist Curt Stern joined the faculty at Berkeley, he found his home in the zoology department with his close colleague, collaborator, and sponsor Richard Goldschmidt; and in 1953, Gunther Stent, who represented the new molecular biology, found his home in the biochemistry department.[138] Thus, while its roots in plant breeding and its agricultural research and teaching mission ensured its continued existence, the division's growth in newer areas was also slowed, if not hampered, by those same historical points of origin. Nonetheless the division survived this transition and Babcock's retirement in 1947, with Clausen replacing him as the chair, and continued to serve integrative functions on the campus especially with respect to orchestrating the graduate

136. These historical terms were introduced by Ernst Mayr. See Mayr and Provine, *Evolutionary Synthesis* (ref. 34). There is no indication that Babcock resented his protégé's success, and in keeping with his commitment to mentoring, Babcock continued to support Stebbins until the time of his death in 1954. Stebbins, in turn, considered Babcock one of the great influences of his career.

137. See Angela Craeger's treatment of the postwar shift in life sciences at Berkeley, its new commitment to biochemistry, and Sproul's correspondence with Warren Weaver. Angela N. H. Creager, "Wendell Stanley's Dream of a Free-Standing Biochemistry Department at the University of California, Berkeley," *JHB* 29 (1996): 331–60; Creager, *Life of a Virus* (ref. 7).

138. See Creager, "Wendell Stanley's Dream" (ref. 137), for more on the biochemistry department, and Creager, *Life of a Virus* (ref. 7), for more on the development of biochemistry on the Berkeley campus and TMV.

program in genetics.[139] By 1959 the department had grown to only seven faculty after Lerner moved into the unit to serve as its chair, but the seven were exceptionally distinguished nonetheless. On the occasion of the centennial of the university in 1968, and the half-century of the department's existence, Lerner could boast that "five of the eleven persons who have served on the faculty have been elected to the National Academy of Sciences, and four have been chosen Faculty Research Lecturers."[140]

The other reason for the slow growth of the unit at Berkeley was the larger directive to build a section of it on the nearby UC Davis campus. To that end, Stebbins was recruited to Davis in 1950 with the directive to organize a section of genetics there. In 1958 it became an autonomous department of its own with the name Genetics. Babcock's initial interests in plants, genetics, and evolution therefore continued to flourish not only at Berkeley but also at UC Davis with his protégé at the helm of a expanding genetics program with a new department and eventually a building of its own.[141]

Babcock's other passion, intimately linked (though in subterranean fashion, perhaps) to plants, genetics, and evolution, found its final expression at the end of his career, too. Stricken with cancer in 1954, a reflective Babcock put his life work into perspective in his final work, a poem he titled a "Cosmolo-Soliloquy [sic]," written in the jittery handwriting of the dying scientist, administrator, and visionary. Described as the "fruitage" of Babcock's mind by his Congregationalist minister, it served as a "radiant expression of the Christian" faith that

139. "Department of Genetics," JAJ (ref. 1). The department also had responsibility for coordinating the teaching of genetics at the undergraduate level across the campus. As the numbers of geneticists grew, so too did the difficulty of coordinating the teaching and avoiding the inevitable competition between units, especially between the Zoology department and the Genetics department. In the mid-1950s things came to a head with botanist Lincoln Constance, then Dean of the College of Letters and Sciences, mediating what was described as a "jurisdictional dispute" between the two units. He formally recommended that the units share teaching in alternate years, but also placed responsibility ultimately with the Genetics department. Negotiations between the units continued at least until the 1960s. I. Michael Lerner to Curt Stern, 27 Jan 1960, JAJ, Box 1, Folder M. Lerner.

140. "Proof from Forthcoming UC Centennial Record," UCGD, Folder Univ. of Cal. Genetics Dept [Galley Proof], Xerox J "Genetics." For one description of the growth of the Davis campus at this time see James A. Jenkins to Mel Green, 17 Oct 1956, JAJ, Box 1, Folder Mel Green. See also Stadtman, *Centennial Record* (ref. 4).

141. For more on genetics at Davis see Stadtman, *Centennial Record* (ref. 4). The photograph chosen for the Centennial celebration and published in the Stadtman collection was the famous portrait by Ansel Adams of G. Ledyard Stebbins and students in the field.

had guided him in his life and work.[142] Read in whole, it was a poetic, reflective, autobiographical rendering of Babcock's complex beliefs, of his own understanding of the grand evolutionary process, and of his own contributions to it. In this too, he was not unlike his counterpart Theodosius Dobzhansky, whose metaphysical beliefs undergirded his interest in evolution.[143] Concluding his life work Babcock wrote:

> Of all the many themes we might discuss,
> It seems to me our nature bent must soar.
> Of all the other lines stretched out before us.
> My one desire, is make my wisdom more,
> And let my understanding grow in range!
> Now basic to this hope is evolution,
> So clearly shown in creatures Earth has born,
> And growth, development and motion
> Must find their base in change; all else is shorn.
> **For Life is Everlasting Interchange!**[144]

ASSESSING THE *CREPIS* RESEARCH PROGRAM: ANALYTICAL PERSPECTIVES AND CLOSING THOUGHTS

Research on the genus *Crepis* began in 1915 with the goal of corroborating Morgan's work on *Drosophila melanogaster* with a plant counterpart. Despite the care demonstrated in selecting *Crepis*, it nonetheless proved unsuitable for this purpose. Research on it instead began to take on a life of its own, serving as an ideal group for the study of complex phenomena observable in plants that had long bedeviled systematists, evolutionists, and geneticists going back to figures such as Darwin and Mendel. Though it was not his original intent, E. B. Babcock thus increasingly took a taxonomic, or more accurately phylogenetic,

142. Wirt, "Babcock: An Appreciation" (ref. 10), 2.

143. For more on Dobzhansky's metaphysics see Costas Krimbas, "The Evolutionary Worldview of Theodosius Dozbhansky," in *The Evolution of Theodosius Dobzhansky,* ed. Mark Adams (Princeton: Princeton University Press, 1994), 179–93; Richard G. Delisle, "Expanding the Framework of the Holism/Reductionism Debate in Neo-Darwinism: The Case of Theodosius Dobzhansky and Bernhard Rensch," *History and Philosophy of the Life Sciences* 30 (2008): 225–46; Theodosius Dobzhansky, *The Biology of Ultimate Concern* (New York: New American Library, 1967).

144. The original handwritten copy is located in a folder titled E. B. Babcock at the California Academy of Sciences. A published version (with a slightly altered title) accompanied the appreciation by Williston Wirt. See Wirt, "Babcock: An Appreciation" (ref. 10).

interest in *Crepis,* until the research program itself became a comprehensive phylogenetic and systematic treatment of it and its closest relatives. So too, the research program as a whole began to take on a life of its own, as more plants were collected by an ever-expanding network, with researchers and students recruited, and as a wider turn to evolution came to interest biologists during the period which saw an amalgamation of Darwinian theory with Mendelian genetics to understand the origins of biological diversity. In 1947 Babcock ruefully recollected: " [I]t was realized that such an undertaking would require a number of years; but it must be admitted that, had the author then appreciated the magnitude of the task, it is doubtful whether he would have undertaken it."[145]

Undertake it he did, however, and by its end the research program could boast a number of novel insights which resolved long-standing issues in plant genetics and evolution, and which represented the new systematics incorporating tools, methods, and insights from genetics, cytology, ecology, biogeography, and even paleontology. Especially important was the articulation of what came to be known as the polyploid complex, a complex of reproductive forms that resolved a number of long-standing problems in plant evolution. With time too, the insights gleaned from the genetics of the evolutionary process in this complex genus helped confirm insights emerging from the "evolutionary synthesis," which in turn helped to consolidate the growing consensus with examples from the plant world.

The research program also helped to inspire a number of additional research initiatives on an international scale as students and researchers recruited to *Crepis* extended its reach. Michael Navashin, one of the earliest students of the genus, helped to spread that influence to the Soviet Union after his return there in 1930 with the creation of a splinter or "offshoot" of the research program at Berkeley. Even more important was the extension of genetics as a whole to the nearby campus of UC Davis in 1950, with the recruitment of Babcock's star protégé, G. Ledyard Stebbins Jr. His own insights into the synthesis of Mendelian genetics and Darwinian selection theory, combined with his knowledge of the research of plant evolutionists and general evolutionists he encountered while Babcock's "junior geneticist," came to fruition in the same year, when his landmark book *Variation and Evolution in Plants* based on his Jesup Lectures was published.[146] It served to organize knowledge of plant genetics and evolution in such a way that it helped

145. Babcock, *Genus Crepis* (ref. 8), 2.
146. G. Ledyard Stebbins, Jr., *Variation and Evolution* (ref. 133).

launch the new science of plant evolutionary biology and consolidate the growing consensus in evolutionary biology. His own career development was enabled by his collaboration with Babcock, which led to his initial appointment at the University of California, a connection he maintained until his death in 2000. A research program that thus grew out of a plant breeding context was slowly transformed—indeed evolved—into a study of plant genetics, systematics, and then plant evolutionary biology involving multiple institutional and national contexts.

As noted, too, a growing agricultural context served as the initial push for Babcock's career and his ambitious research program, though the plant itself had no discernible agricultural use. Nonetheless, the *Crepis* project helped build genetics on the UC Berkeley campus with notable strengths in plant genetics in general and evolutionary genetics in particular, making the unit a veritable "mecca for evolutionists" all over the world in the critical first few decades of the twentieth century. Though genetics rapidly outgrew its agricultural origins at Berkeley, as elsewhere, it continued to flourish in those same contexts, spreading offshoots especially on campuses such as UC Davis.

Thus, what began as an attempt to search for a plant counterpart *Drosophila melanogaster,* an ideal living organism that would illuminate the mechanism of Mendelian heredity in the plant world, became an enormous undertaking to understand the phylogeny of an especially complex group. As an ideal organism for genetics, *Crepis* proved to be less than perfect, but as a group for understanding the genetic basis of evolutionary change in a complex representative of the plant kingdom, it proved to be close to ideal. It was not in fact the plant counterpart of Morgan's classical genetics research on *Drosophila melanogaster*; it was the plant counterpart of Dobzhansky's studies of the genetics of natural populations in *Drosophila pseudoobscura* and its close relatives; and the success of the *Crepis* program, as noted by Jens Clausen, perhaps exceeded even that.

Finally, this historical study offers some interesting insights for historians of modern biology who follow the recent literature on experimental systems, model organisms, and research programs. In this literature, the genus *Crepis* might been seen to function as a kind of experimental system, taking on a life of its own within a research program that shifted directions unexpectedly from experimental genetics to evolutionary biology. In this reading, the paper has traced how the system was articulated, how it shaped a kind of scientific culture, and how it generated and then ceased to make "epistemic novelty."[147] But while

147. I am referring here to the description of experimental system as articulated in Hans-Jörg Rheinberger, *Toward a History* (ref. 6).

helpful, such a focus on the system or on *Crepis as a system* makes for only part of the story, and an incomplete, if not distorted one at that. Babcock's study of the genus was at first based on the desire to corroborate the kinds of claims made as a result of experimental studies of *Drosophila melanogaster*, but the epistemic novelty in genetics soon proved itself limited in *Crepis*. Instead, the system began to demonstrate its utility to understanding historical processes like evolution; in that process, *Crepis* itself became the object of study—how it came to be, how it sustained its relationships, and where it was located in time and place. In that sense, it was not a "model organism," in any conventional sense of the phrase, though it did eliminate or diminish confusion over which evolutionary mechanisms operated in the genus as well as providing a workable methodology for understanding the evolution of complex plant genera like it. Study of the genus thus involved a more specific historical reconstruction and the kind of inferential and indirect reasoning that characterized natural history–oriented sciences rather than laboratory or instrument-driven experimental sciences shaped more readily "experimental systems," or "model organisms"; and while the laboratory or greenhouse or garden served as places for varied kinds of experimental study, the natural settings that had given rise to *Crepis* and had sustained it and its close relatives for thousands if not millions of years were equally if not more important to understanding its evolutionary history.

The genus *Crepis* thus became the ideal organism of study for the growing evolutionary community looking to a general understanding of the genetic basis of evolutionary change, but one that also included the kinds of historical or environmental particularities commonly associated with taxonomic groups. *Crepis* thus can be seen to function as a kind of resource for Babcock and his group because it provided historical and geographical knowledge that could be followed at the level of the gene (or the chromosome, to be more precise), but that also served to eliminate alternative or rival accounts entertained by evolutionists at the time. Babcock's turn to evolutionary study, from his initial commitment to the mechanistic study of heredity, was thus in part due to the fact that his system was providing him with more reliable knowledge, but it was also in part because it provided him with the opportunity to fulfill a number of long-standing interests that included integrating botanical study, genetics, and evolution, and all against a view of progressive evolution. That he was able to not only sustain these early interests but to bring them to fruition with his research on *Crepis*, was also enabled by the shifting administrative needs of his institutional base in a state following a specific agricultural and sociopolitical program. The "experimental system" mattered, to be sure, but so too did a range of other factors including Babcock's own undergirding religious beliefs or metaphysical commitments of which we know little, his ambition as researcher, his vision as administrator, his institutional backdrop, and the State of California, as well as the "grand theory" driving the modern synthesis of evolution. The research program thus did not take on just *any* life; it was a life embedded within a historical context that simultaneously enabled and constrained it.

For historians of biology, furthermore, study of E. B. Babcock, the genus *Crepis,* and the evolution of his research program at Berkeley might encourage a rethinking of the appropriateness of the phrases "experimental system" and "model organism" for general historical study of modern biology. Both have led to productive insights especially in histories of the biomedical sciences and have provided reliable accounts of instrument-driven, experimental sciences. But both need to be properly historicized and situated in more recent developments in the biomedical sciences rather than applied to the history of modern biology as a whole.[148] As this historical reconstruction based on documents generated by historical actors such as E. B. Babcock has shown, the phrases "model organism" and "experimental system" never occurred once in the historical record, let alone been applied to *Crepis.* It was instead considered an "ideal form" for genetical study. Such attention to the language of historical actors through archival or published records helps us appreciate the far more complex role that organisms played in the history of biology during the first half of the twentieth century.[149]

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148. By "biomedical" I also include histories of molecular biology, biochemistry, and some histories of genetics. See, for example, Robert Kohler, *Lords of the Fly* (ref. 7).

149. For more discussion on the historiography of biology, see Smocovitis, *Unifying Biology* (ref. 34).