Descended from Darwin

Insights into the History of Evolutionary Studies, 1900–1970

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Chapter 2

"The View-Point of a Naturalist"

American Field Zoologists and the Evolutionary Synthesis, 1900–1945

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The decades before the evolutionary synthesis have repeatedly been described as a period of confusion that resulted in a long delay in the synthesis of Mendelian genetic theory with Darwinian evolutionary theory. As Ernst Mayr has long contended, the delay of the synthesis was due mainly to the communication gap between experimental geneticists and (field) naturalists. The consequences of this were that geneticists ignored the literature on geographical variation and speciation, while the naturalists neglected the advances in genetics. Historians have begun to examine how this gap was finally bridged in the work of several individuals, including Francis Sumner, Sewall Wright, and Theodosius Dobzhansky. Others have studied how the required "community and research infrastructure" for the establishment of a discipline of evolutionary biology was put in place in the late 1930s and 1940s and how Mayr played a prominent role in this process.[1]

There can be no doubt about the central role played by Mayr in the renovation of evolutionary studies in America. He was a tireless promoter and organizer, as Cain (1994, 2002) has shown. Mayr aggressively took over a variety of fledgling organizations to advance his own view of what the evolutionary research community ought to look and act like. This "personality factor" and Mayr's location in New York, in close contact with Dobzhansky, Simpson, and other like-minded biologists, helps to explain his prominence among systematists involved in the synthesis. But we also need to explore other contributing factors.

The difference in training between German and American systematists in the early twentieth century seems to be important in this respect. From Mayr's own recollections and Harwood's work on the German genetics community, it appears that the importance of communication and cooperation across specialties had an institutional foundation and was appreciated by both geneticists and systematists.[2] Jürgen Haffer has noted how Erwin Stresemann, Mayr's teacher, worked to turn ornithology into a branch of modern biology, stressing the importance that his students receive a broad biological training (Haffer, 1994).

In contrast, the institutional separation between field naturalists and geneticists in the United States was exacerbated in the early decades of the twentieth century, posing an obstacle to cross-disciplinary cooperation. Mayr described the gap between systematists and geneticists as one between scientists inhabiting different "conceptual worlds." Systematists thought in terms of phenotypes and populations, while geneticists lived in a world of genotypes and exhibited typological thinking. As a relatively recent German émigré, arriving in New York in 1931, Mayr was not very familiar with the events taking place in the American biological scene during the early decades of the century. Not being a member of the community of field zoologists, but a recent arrival, he could see the conceptual problem, but not how it had become institutionally embodied.

The very centrality of Mayr as *both* the main *advocate* of systematics during the synthesis period, and the main *historian* of the role of systematists and systematics in the synthesis has led us to neglect the geographical, institutional, and intellectual diversity that was present within that field, as far as new developments in the revival of evolution are concerned. Cain noted this very problem, warning us that the "prominence . . . of the New York Circle" of evolutionists could become an obstacle to a "more comprehensive understanding of the synthesis period." A focus on "organizers and promoters," he continued, might obscure the attitudes and activities of the "rank and file" of the evolutionary research community. To avoid these perils he encouraged historians to produce detailed studies that explore the diversity within the emerging communities (Cain, 1993, pp. 24–25).

A first step in this direction is to revisit the "dark ages" that preceded the mid-twentieth century rebirth of evolutionary biology. It is imperative that we analyze in detail the nature of the withdrawal from evolution noted by historians. We must reexamine the clashes between systematists and geneticists around 1900. To what extent, if at all, did American field zoologists participate in this retreat during the first decades of the century? What kind of contributions did they make to the synthesis?

No professional discipline or other community infrastructure for the study of evolution was established in the early decades of the twentieth century. Nevertheless, it is revealing to examine attempts by field naturalists to establish research programs in evolution during that period. These efforts increased the interest in speciation that put in motion the organizational developments of the 1930s. Hence they contribute importantly to the transforming traditions within systematics during the first decades of the century. Several institutions established (or revived) in the first years of the century became important centers for work on geographical variation and speciation during the 1920s and 1930s. Located in California and the Midwest, these institutions allow us to move beyond the almost exclusive focus on New York and the Dobzhansky-Mayr-Simpson axis.

This change of focus also will emphasize the diversity of *attitudes* toward experimental work in evolution in the presynthesis period. It also highlights the diversity of *activities* conducted by field zoologists in their attempts to regain centrality and prestige as evolutionists. This entails exploring in greater detail the supposed nonexistent relationships between geneticists and members of other biological specialties in the decades previous to the synthesis. It also means examining the role played by systematists other than Mayr in facilitating the growing conversation across the biological disciplines.

In the first section of this chapter I review the clashes between field zoologists and experimental evolutionists during the first decade of the twentieth century. My objective is to bring to the foreground how the relationships between these two groups of biologists were influenced by two particular events during the 1900s. These events included the new opportunities for research support offered by the Carnegie Institution of Washington (CIW) and the debate over the role of isolation in evolution. In the following sections, I analyze three cases of changing attitudes of field naturalists toward experimental approaches to the study of evolution during the 1910s through the 1930s. They took on the themes of geographical variation and speciation and transformed systematic work for decades to come, paying particular attention to ecological themes and introducing statistical and experimental methods. Next, I examine the collaboration between Francis Sumner and Joseph Grinnell, a collaboration that helped Sumner achieve his synthesis of genetics and systematics in the 1920s. Finally, I review the role played by Carl Hubbs as editor of the "Reviews and Comments" section of *The American Naturalist* during the 1940s. Together, these contributions highlight the institutional diversity and the heterogeneity of the activities and attitudes that existed within the community of American field zoologists before and during the evolutionary synthesis. This serves to complement existing studies of the role played by Mayr.

Clashes in the 1900s: Biometrics, Mendelism, and Field Zoologists

As the nineteenth century drew to a close, the emergence of such movements as biometrics, mutationism, and Mendelism sent many biologists into an aggressive competition for authority regarding evolutionary processes. Among American zoologists, the emerging epistemological division between field workers and the advocates of experimental methods developed into a separation at the institutional level with the appearance of the CIW as a new patron for scientific research.

The existence of a separation at the level of scientific practice was manifest in embryologist E. B. Wilson's famous address on the "Aims and Methods of Study in Natural History" in 1901. Wilson remarked that, during the last decades of the nineteenth century, "a lack of mutual understanding existed between the field naturalist and the laboratory workers which found expression in a somewhat picturesque exchange of compliments, the former receiving the flattering appellation of the 'Bug-hunters,' the latter the ignominious title of the 'Section-cutters,' which on some irreverent lips was even degraded to that of the 'Worm-slicers'!" (Wilson, 1901, p. 19). As befitted a presidential address at the annual dinner of the American Society of Naturalists, he tried to emphasize that a certain rapprochement was taking place, and he called for a multiplicity of methods as the best way to advance biological science. That such a topic took center stage during the last meeting of the century was a clear sign that the differences he was trying to minimize existed and undoubtedly were present in the minds of life scientists.

With naturalists on edge, biometry appeared as a reform movement able to make possible an *entente cordiale*. In the United States, the biometrical movement was championed by Charles Davenport and other biologists who had come of age in the morphological laboratories of the 1890s. Its advocates saw biometry as a way of using the new set of experimental and quantitative tools for the study of evolution. As biometrics required a certain commitment to field research, this movement seemed capable of bringing together zoologists from both sides of the divide. As a matter of fact, biometrics managed to temporarily attract some of the young field zoologists who entered the landscape of biological science in the 1890s and 1900s, such as Carl Eigenmann and Charles Adams. These young biologists saw in it a modern continuation of the studies on geographical distribution and variation conducted by the previous generation of field zoologists between the late 1860s and the 1890s.

However, the rhetoric that accompanied early statements by biometricians was not a call for collaboration on an equal basis. The new approach was publicized as a means to redefine and subordinate, rather than complement, field scientific practice. As a consequence, it managed to alienate many field naturalists. A clear example of this attitude is found in William Bateson's early work. Although known as a foe, rather than a practitioner, of biometrics in the late 1890s, Bateson called for the "statistical study of wild specimens" as the starting point of the experimental study of evolution. He urged the cooperation between two kinds of biologists, the "evolutionist" and the "collector" (Bateson, 1897–1898). This collaboration was an unequal partnership: collectors were asked to do the lowly fieldwork that served as a foundation for experimental investigations by real (i.e., laboratory-trained and based) evolutionary biologists. In the United States, Davenport also offered a statistical redefinition of the practices of systematists and field naturalists, arguing for a statistically formulated "precise criterion of species" and for the establishment of "place-modes"[3] for species (Davenport, 1898, 1899). Like Bateson, he too solicited field naturalists to work along the lines he proposed. Field naturalists, especially those from older generations, resented these attempts to reformulate their concepts, redirect their practices, and turn them into mere providers of raw data for the work of the true evolutionists. Such terms made any lasting collaboration impossible.[4]

The existing wedge between field and laboratory zoologists was driven further with the establishment of the CIW and the ensuing competition for this new source of funding. When the CIW invited applications for grants in 1902, several field zoologists responded enthusiastically. They proposed a series of surveys to complement in various ways the collecting work conducted by several generations of systematists during the second half of the nineteenth century. Zoologists including David Starr Jordan, C. Hart Merriam, Gerrit Miller, and Leonhardt Stejneger—leaders in their respective systematic fields of ichthyology, mammalogy, and herpetology—welcomed CIW funding as a means to expand their collections beyond the North American continent and, in the process, elevate the perceived low caste of taxonomy. Carnegie funds could be used, for instance, to train a new generation of students and to bring some uniformity to the chaotically disperse literature of systematics. From the outset, however, the CIW's Advisory Committee on Zoology leaned toward Davenport's plan for an experimental station for the study of evolution. Merriam, a member of the committee, expressed his doubt that the study of such a complex and central problem as evolution could be conducted through "a single laboratory by the sea." Instead, he favored the establishment of diverse methods and institutions as the most appropriate way to study such a fundamental issue.[5] Yet whereas the survey proposals mentioned evolution only as an afterthought, a mere by-product of taxonomic or survey work, Davenport's proposal placed evolution at the very center. Not surprisingly, the systematists did not receive any funding for their surveys, while Davenport got financial backing for his station and became the CIW's main adviser in zoological matters.

Field zoologists quickly expressed their dissatisfaction with the ways the CIW funding policies were fueling existing trends toward the reduction of zoology to laboratory work and of evolutionary studies to experimental evolution. This dissatisfaction was brought to the foreground in the exchanges between ichthyologist Carl Eigenmann and CIW officers regarding Eigenmann's requests for research funds. An ichthyologist who studied under Jordan at Indiana University, Eigenmann (PhD, 1889) had submitted two grant proposals for the study of the origin of blind fishes and of the South American fish fauna. As these were turned down in 1904, he sought an explanation from CIW officers. The official response followed the advice of the reviewer of the proposals, Davenport, who stated that "systematic," "faunistic and geographic work" should not be funded by the CIW, since it had "a minimum of utility" and was "the special province of museums."[6] Eigenmann pressed Robert Woodward, the institution's Secretary, for the creation of a department that would focus on the subjects of "distribution, genealogy, and variation," through which those who wished to study evolution nonexperimentally could be supported. He accompanied his petition with a series of letters from like-minded zoologists, but to no avail.

Another incident with the CIW left Eigenmann fuming. In his (unsuccessful) proposal to study blind fish, he had asked for funds to support one of his students, Arthur Banta. A few years later, Banta received CIW funding through Davenport's station. While Eigenmann's research in natural caves in South America and Indiana had been rejected, he learned that Davenport was building an artificial concrete cave for Banta's work in the basement of the station's lab. Eigenmann could not believe that zoologists would have such disregard for the study of animals in natural conditions and that the CIW would support such an attitude. In his final letter to Woodward, he angrily insisted that "the study of Evolution is possible to others than the 'cocky' experimentalists" that the CIW had decided to support.[7]

Other field research in zoology directed at the study of evolution was funded by the CIW at the beginning of the century, but even in those cases funding was granted because of the credentials of the grantees as laboratory zoologists. William L. Tower, whose results on the potato beetle were eventually found to have been faked, was a student of Davenport who specialized in experimental studies on the physiology and development of coloration. Henry Crampton was also a product of the morphological laboratory: a student of E. B. Wilson who worked on the inheritance of color in Lepidoptera before turning his attention to *Partula* snails.

Thus, the immediate effect of early CIW funding in zoology was to offer institutional reinforcement for the widening cleavage between experimentalists and field naturalists. Its policies increased the sense of alienation already felt by nonexperimental biologists, who saw that their work was unlikely to receive financial help from outside their own institutions. And, as most of these institutions happened to be museums, CIW policies sanctioned the separation between museum work and research done in laboratories and biological stations. Museum workers, who were to be exclusively supported by their own institutions, had one less incentive to interact with other life scientists outside the museum world.

In addition to the protestations of field naturalists, a more serious problem with biometrics involved the promise of Mendelism. This led Davenport and other quantitatively minded biologists quickly to abandon biometrical studies for breeding experiments. After all, Davenport's advocacy of biometry was founded on its being a *quasi-experimental* practice. "As by experiment we make all causes similar except one and note the result," he argued, "so in statistics we select results having at least one common cause and throw all together, believing that, from the doctrine of chances, all other causes will offset and annul each other. Thus we find, by comparing the mean in the selected group with the mean of the whole population, the effect of the particular cause used as a basis of selection" (Davenport, 1900, p. 267). For a mathematically skilled naturalist, the manipulation of quantitative data could be compared to the actual experimental manipulation of organisms.

The appearance of de Vries's *The Mutation Theory*, with its espousal of crossing experiments, contributed to a quick abandonment of biometrical study. In his review for *Science*, Davenport emphasized how de Vries's work was the response that many experimental biologists were expecting to the existing "need of a revolution in [the] method of attacking the problem of evolution." Beyond the particulars of his theoretical solution, Davenport argued, "the great service of de Vries's work is that, being founded on experimentation, it challenges to experimentation as the only judge of its merits. It will attain its highest usefulness only if it creates a widespread stimulus to the experimental investigation of evolution" (Davenport, 1905, p. 369). Why use pseudo-experimental techniques when truly manipulative methods could be applied? Experimental breeding immediately superseded biometrical studies as the method of choice for Davenport and many other experimental biologists interested in evolution.[8]

The problem was that this move away from biometry signified also a withdrawal from the study of evolution. Or, if not immediately a withdrawal in Davenport's eyes, it certainly represented "a new formulation of the problem" of evolution. At the turn of the century, the problem of organic evolution and the problem of the origin of species were deemed one and the same problem; a decade later that had changed. "We think less of the origin of species and more of characteristics," Davenport claimed in 1912. The modern study of heredity had further refined the problem of evolution as that of "germinal determiners of characters" (Davenport, 1912, p. 129).

The mutationists were trying to take the space and time dimensions out of the evolutionary process, hoping to make evolution susceptible to experiment, and to experiment only. For field zoologists, this was unacceptable. Davenport argued that, in addition to provoking a reformulation of the problem of evolution, the experimental study of heredity had shown the "relative unimportance" of isolation (Davenport, 1912, p. 138). Yet an emphasis on isolation was exactly the response of field zoologists to the appearance of the mutation theory. In 1905 D. S. Jordan took exception to the evidence and methods brought to evolutionary study by de Vries and his followers. Jordan resurrected the notion that geographical isolation was necessary for the formation of species, and situated that concept at the center of the cleavage between "every competent student of species or of the geographical distribution of species" and "those who approach the subject of evolution from some other side" (Jordan, 1905, p. 545). Jordan relied on fellow systematists to offer evidence against de Vries and other advocates of experimental evolution. Field zoologists knew that regions with a large number of barriers were characterized by a great number of related species, usually having narrow ranges. Conversely, regions with few barriers, in which migration and interbreeding were possible, presented homogeneous faunas with few, widely distributed species. Barriers prevented interbreeding between populations with potential differences in the parent stock. These populations could be subjected to different environmental conditions creating different selective pressure. The mutationists' evidence (of parent and daughter species existing side by side) contradicted this generally accepted zoogeographical evidence.

Those who came to the defense of de Vries's methods, especially Davenport and the botanist Daniel MacDougal, called for breeding experiments as the ultimate tests, claiming that what was at stake was a correct understanding of the physical basis of inheritance and variation. "Taxonomic and geographic methods" (i.e., "consideration of fossils, herbarium specimens, dried skins, skulls of fish in alcohol") were irrelevant; what mattered was the mechanism behind the transmission of characteristics from generation to generation (MacDougal, 1906, p. 224; Kingsland, 1991). Evolution was a genic phenomenon to be studied with genetic experiments. As Jordan and those who agreed with him did not seem prepared to accept this view, the advocates of experimental evolution quickly returned to their studies of heredity and ignored the field naturalists' arguments. For field zoologists, the debate was more productive, leading to a clarification of the concept of "barrier" and to the coining of the concept of "speciation" as different from "evolution."[9] However, the net effect of the debate was to turn each group inwards, with field zoologists taking isolation and speciation as the central subjects of their evolutionary studies and experimentalists focusing exclusively on hereditary mechanisms.

Field Zoology in the Early Twentieth Century

The debate on isolation illustrated that field zoologists and experimental evolutionists or geneticists had different views on what the significant dimensions of evolution were and how to study them. Field zoologists who entered graduate school at the beginning of the century received the full impact of this debate, and their response was different from that of the geneticists. This is evident in the early careers of two of the most prominent members of this generation, Charles Christopher Adams (PhD, University of Chicago, 1908) and Joseph Grinnell (PhD, Stanford University, 1913). The research programs pursued by these zoologists centered precisely on a defense of the role of geography-space and history-time in the evolutionary process, the two dimensions generally neglected by the advocates of experimental evolution. Methodologically, they sought to improve upon what they perceived as the "static" nature of previous natural history. On the institutional plane, they envisioned reforms based on the redefinition of the regional natural history museum as an instrument of research in evolution.

Charles C. Adams (1873–1955)

Adams did graduate work under Davenport at Harvard and Chicago beginning in 1898. He intended to develop biogeography into a dynamic science by drawing from the most modern approaches in biology and geology. Following Davenport, he used biometry to study the correlation between variation and geographical distribution, focusing on the distribution of the molluscan fauna of the Tennessee River (Adams, 1900, 1915). He combined this with a study of physiographic forces (erosion, base leveling, migration of divides, river capture) that provided the geographical dynamics behind the evolution of the environment.

Adams wanted to carry out a reform in the practices and professional activities of field zoologists. If they were to be relevant in the quickly changing landscape of biology, field zoologists had to abandon old-fashioned practices and theories. One way of doing this was to draw from the resources other disciplines (such as geography) were developing. Adams advocated an "ecological method in evolutionary study." He claimed that if the study of evolution had not advanced more rapidly it had been because naturalists had failed "to analyze dynamically environmental complexes" and their role in evolutionary change.[10] He saw himself and other field naturalists as participating in a "geographical move" in the study of evolution. With its focus on the study of isolation and the dynamic study of habitats, this was to be the foundation of further experimental work. Only with a combination of approaches would the study of evolution move ahead.[11]

Adams also fostered a series of organizational and institutional changes directed at the development of a sense of community among field zoologists and the improvement of the image of field zoology. Among other initiatives, he encouraged the active participation of field zoologists in the organization of the Association of American Geographers. His hope was to promote new dynamic methods in biogeography; he called for the introduction of new exhibit and research practices in natural history museums, including the gathering of pedigree cultures used in breeding experiments by geneticists. He defended the contributions by field and museum naturalists to evolutionary study. In his view, the role of natural history museums was "to illustrate and investigate the evolutionary processes of the earth with special reference to the interrelations of organisms and their environment."[12] Adams pursued this goal during his brief but influential tenure as curator of the University of Michigan Museum of Zoology.

Joseph Grinnell (1877–1939)

On the West coast, Grinnell showed a similar interest in advocating a geographical perspective and embodying it in a museum. Grinnell did his graduate work at Stanford University, under Jordan's student Charles Gilbert. Although his training emphasized taxonomy over laboratory work, he also was introduced to the study of heredity and development during his graduate school years.[13] As a graduate student, Grinnell already was interested in making research in ornithology more relevant for the investigation of evolution (Grinnell, 1902). His work used information on the size and character of the ranges of species and subspecies as evidence to explain evolution as an effect of historical changes in environmental conditions. During the 1910s he developed a research program devoted to studying the role of barriers and isolation in evolution.

As director of the Museum of Vertebrate Zoology (MVZ), established at the University of California in 1907, Grinnell advanced this research program through a series of surveys of several regions in California that offered topographical and faunal peculiarities. In the research conducted by the MVZ he developed a uniform system of specimen collection and field notes designed to make possible an historical evaluation of the effect of the dynamics of the environment on faunal change.[14] For Grinnell, the careful study of the distributional ranges of animals provided evidence for a historical reconstruction of the process of the origin of species. Describing this work as "dynamic zoogeography," he called his method "comparative distribution": the comparative study of the ranges of animals, as the means to investigate the role of barriers and isolation in evolution (Grinnell, 1914). Like Adams, he saw the reduction of evolutionary studies to books on mutation and inheritance as a misguided effort on the part of geneticists. The problem of the origin of species belonged at least as much to the geographer and the systematist as to the student of heredity.

Larger Significance of Grinnell and Adams

What was the significance of these lines of research opened by field zoologists such as Adams and Grinnell in the first two decades of the century? Answering this question requires an examination of field zoology during the 1920s and 1930s. Adams and Grinnell may have had little direct involvement in the emergence of the synthesis in the 1930s and 1940s, but they left their mark on two institutions that produced a number of contributors to that synthesis.

At first, one may be tempted to point at their failure in creating a discipline of evolutionary ecology. Instead of taking evolution as its organizing principle, the then-emerging discipline of ecology became the field physiology advocated—among others—by botanist Frederic Clements and zoologist Victor Shelford. Shelford was forced to choose between evolution and physiology as the organizing principle for ecological science. A physiographic approach could explain animal distribution from a historical perspective, while a physiological approach had to be built on the experimental investigation of animal responses to environmental factors. Shelford opted for physiology in his attempt to make ecology more legitimate. With this move, he became the main representative of animal ecology in America and set the discipline in a direction similar to that taken by its botanical side under Clements. Although Adams continued to seek a way to integrate both perspectives, he failed to make his interest in historical approaches to distribution advance his career. He was forced to move into the field of conservation and wildlife biology.[15]

More important for our studies of the synthesis, however, is the effect that Adams had at the institutional level. He reorganized the University of Michigan Museum of Zoology, bringing it back to life in the early 1900s. Although his tenure at the museum was short, his student and successor, herpetologist Alexander Ruthven, maintained Adams's legacy. Ruthven imbibed from Adams a sense that systematic work had to go beyond its descriptive phase and be directly involved with the investigation of the origin of species. In Ruthven's own words, it had to be done "upon a geographic basis," adopting "statistical methods" (Ruthven, 1908, pp. 2, 8). Under his tenure, first as curator and then as director, the policy of the museum emphasized "intensive environmental studies" and their role in the study of evolution, reflecting Adams's teachings. "The course of evolution in a group can never be demonstrated by analytical systematic work," Ruthven stated; "synthetic results can only be relied upon when supported by a knowledge of the geographical history of the group, and environmental relations are a potent factor in geography" (Ruthven, 1917). Following this policy, the expeditions conducted during the 1910s sought to investigate the effects of isolation and a host of topographical conditions on mountain fauna.

Around 1920 Ruthven recruited two young field zoologists who gave the museum a considerable strength beyond herpetology and situated it as one of the most prominent centers for field zoology in the United States. One of them was Lee Dice (1887–1977), a mammalogist who received his PhD from the University of California, Berkeley, in 1915. The other, Carl Hubbs (1894–1979), was an ichthyologist of the Jordan school (MA, 1917, Stanford University; PhD, 1927, University of Michigan). For two decades, Dice and Hubbs became two of the main contributors to the study of speciation in the United States from the point of view of field zoology.

Carl Leavitt Hubbs (1894–1979)

Carl Leavitt Hubbs's early work was directly connected to the investigations conducted in previous decades by Carl H. Eigenmann and his students on local variation. This work focused on the study of correlations between environmental conditions and meristic variation (variation in the number of vertebrae and other segmentally arranged structures in fish). Following the lead of the German zoologists Friedrich Heincke and Johannes Schmidt, Hubbs turned to the correlation between developmental rate and the number of segments produced (Hubbs, 1922). In his doctoral dissertation he explained these structural modifications that characterize different local races of fishes, as the result of physiological adaptations (and, thus, as indirectly adaptive) (Hubbs, 1926). Beginning in the late 1920s, he conducted breeding experiments to prove the genetic nature of some of these morphological differences between populations. From this work he moved into the study of hybridization in speciation.

In pursuing these studies, Hubbs was incorporating experimental methods into his systematic work, a step beyond Eigenmann's initial embrace of statistical methods. Hubbs had been, since his student days at Stanford, a strong advocate of the need to pursue studies of local races in parallel to the work conducted by geneticists. In 1934 he introduced the term "new systematics" to refer to this field where "genetics can not replace variation investigations . . . because systematic groups are populations, and must be investigated by population analysis" (Hubbs, 1934, p. 116). Characteristics of this new systematics were the use of distribution, habitat, habits, and life history, as well as statistical and experimental (tagging and transference experiments) methods.

Lee Raymond Dice (1887–1977)

Hubbs's colleague for over twenty years at the Museum of Zoology, Dice is remembered as the successor to Sumner for studies on *Peromyscus*.[16] The only personal link between these men involve the mice themselves: Dice received Sumner's *Peromyscus* stocks after Sumner discontinued his research in the late 1920s. Dice's work between the mid-1910s and mid-1920s was ecological. It focused on the distribution, life histories, and habits of mammals in the Northwest and the Midwest, and showed little or no interest in evolution. For instance, when in 1921 he submitted a proposal to the CIW, he asked for funds to do the necessary fieldwork to correlate animal distribution with vegetational associations. (The proposal was unfavorably reviewed by Clements and duly turned down.)[17]

In 1923 Dice brought some deer mice from an expedition to northern Michigan and began to breed them, adding other stocks from expeditions to Colorado in the following years. Three years later he submitted a new proposal to the CIW, but this time the topic was "Studies of the Factors Determining Speciation in Mammals and Reptiles." Dice proposed to conduct transference experiments between Michigan and Arizona (using *Peromyscus*, as well as various races of snakes and lizards) and also hybridization experiments with snakes and deer mice. Two secondary projects involved studying the influence of climate on the reproductive physiology of mammals, and the relations between environment and growth in reptiles.[18]

The CIW's help did not materialize until the early 1930s, after Sumner had abandoned his own *Peromyscus* studies. Beginning in the mid-1920s, Dice's *Peromyscus* research focused on the study of geographical variability in several species, the analysis of the degrees of interfertility between species and subspecies, and the role of ecological isolation (Dice, 1933, 1940a, 1940b; Dice & Blossom, 1937). These *Peromyscus* studies during the 1930s and 1940s involved not only some of his own students (e.g., Adolph Murie [PhD, 1929]; William F. Blair [PhD, 1938]) but also several other associates of the museum (Philip M. Blossom; William H. Burt [PhD, 1930]).

By the late 1930s, the combined efforts of Hubbs and Dice on speciation problems had made the University of Michigan, in the words of Theodosius Dobzhansky, "a center of this type of work, which is so rare in general." When in 1939 the American Association for the Advancement of Science, the American Society of Zoologists, and the Genetics Society of America organized two symposia on speciation, Hubbs and Dice were the only two field zoologists besides Mayr to deliver a paper.[19]

At the MVZ, Grinnell's footsteps were followed by a large group of field zoologists. E. Raymond Hall (PhD, 1928), Alden Holmes Miller (PhD, 1930), and Seth Benson (PhD, 1933) pursued studies of geographical variation and speciation during the 1930s. They also participated actively in the discussions that led to the establishment of the Society for the Study of Speciation in 1939. Particularly significant was the work of Alden Miller on habitat selection as an isolating factor and on population differences between subspecies of *Junco* (Miller, 1941). He became responsible for the ornithological collections and director of the museum after Grinnell's death in 1939, while Benson was curator of mammals. Other associates of the MVZ who contributed studies with relevant speciation information were Jean M. Linsdale (PhD, 1927) on sparrows, Robert T. Orr (MA, 1931) on rabbits, William H. Behle (PhD, 1937) on larks, Henry S. Fitch (PhD, 1937) on garter snakes, and Barbara D. Blanchard (PhD, 1939) on sparrows.

The legacy of Adams and Grinnell was a philosophy of museum work that members of later generations imbibed at Michigan and Berkeley. This was one of the ways in which American field zoologists from the early twentieth century contributed to the discipline of evolutionary biology that emerged in the 1940s. While studies of the synthesis have (rightly) focused on "architects," we still need to learn more about other participants in the process, the links that tie them to previous generations, and the differences between members of successive generations.

Collaboration Between Sumner and Grinnell

In addition to emphasizing dynamic zoogeography and speciation studies, Adams and Grinnell instilled in their students the notion of complementarity. Their work, together with contemporary studies of heredity, were complementary efforts towards the shared goal of understanding evolution. They incorporated this spirit of cooperation into the philosophy of their museums. Grinnell also put that spirit into practice by cooperating actively with an experimental biologist, Francis Sumner. In this section I analyze how this cooperation contributed to Sumner's early synthesis of genetics and systematics.

Traditional accounts of the synthesis represent Sumner's work as the beginning of a reconciliation between field and laboratory zoologists. According to William Provine, Sumner was "a major figure in the development of twentieth-century evolutionary thought" who "bridged the gap between genetics and systematics, a major step toward the evolutionary synthesis" (Provine, 1979, pp. 211, 212). Mayr described Sumner as one of the naturalists responsible for population systematics, as well as a pioneer of population genetics (Mayr, 1980a, p. 31). Both Mayr and Provine characterized Sumner as a "naturalist" (in Mayr's charged sense of the word) (Mayr, 1980b, p. 129) and "mammalogist/systematist" (Provine, 1979, p. 228). Provine notes how Sumner defied simple characterizations, quoting his subject directly: "Dr. Sumner calls himself a geneticist when he is sure no geneticists are within hearing; also a mammalogist when no mammalogists are present. He is admitted to the fellowship of neither, and has some of the intellectual vices of both" (Provine, 1979, 211; no source given). This quotation suggests Sumner was relatively uncomfortable with *each* of these groups, and he sought communication with *both sides*. This does not say much about his self-identification.

I think another attempt by Sumner at self-description is more revealing. In a letter to D. S. Jordan in 1923, he confessed,

> The geneticists, or many of them, seem to regard such methods as I employ as quite "uncritical" and inconclusive, so far as the problems of heredity are concerned. On the other hand, many of the taxonomists seem to resent the intrusion of a "laboratory" biologist into fields that they believe to be their own exclusive property. So I am between two fires, or more commonly, both camps ignore my line of evidence altogether.[20]

Sumner saw himself rather as a wayward or anomalous geneticist who had sought—or, perhaps more accurately, been thrown into—the company of systematists.

As a student in the 1890s Sumner's training was as a morphologist, first under Henry Nachtrieb at the University of Minnesota and later under Bashford Dean and E. B. Wilson at Columbia University. This training included the customary summer visits to the Naples Zoological Station and the Marine Biological Laboratory at Woods Hole. The mark of this training is noticeable in his complaints about his job as director of the laboratory of the U.S. Bureau of Fisheries (since 1903), which occupied him on a survey of the Woods Hole area. It was only out of necessity that he accepted to conduct this survey work, which was, in his opinion, purely descriptive and clearly "low grade." He believed that, in evolution, the important facts were "being investigated by the modern 'experimental' school of biology" (quoted by Provine, 1979, p. 215). He saw the future of evolutionary study in biometry.

Ten years later, however, Sumner was not as sanguine about this modern experimental cadre of evolutionists. Biometry had been abandoned, replaced by what Sumner called "the Mendel-deVries-Johannsen school of evolution." The followers of this new school of experimental evolution thought "species formation consists in various new combinations of existent unit characters" that could be manipulated in hybridization experiments. This approach neglected, in Sumner's view, the effect of the environment. In contrast, Sumner took an interest in the work of "systematic mammalogists" who studied geographical races of the same species occupying slightly different habitats. The proper experimental studies in evolution, Sumner now thought, were not being done by "those who enjoy the facilities for this work in our country" (e.g., Davenport), and it was systematists who seemed to be working on the appropriate materials for experiment in evolutionary study.[21]

As Provine has pointed out, Sumner had "scientific, philosophic, and emotional objections to the new genetics" that had developed at the time. Sumner's newfound interest in the work of systematists began as a consequence of his Woods Hole survey work. As preparation for his Woods Hole report, Sumner engaged in a comprehensive review of the literature about the fauna of the New England coast. This acquainted him with the work of naturalists conducting field researches for the Bureau of Fisheries (formerly the U.S. Fish Commission) in that area. In other words, his professional situation outside the university forced him, a laboratory biologist, to look into the work of field zoologists. In addition to his growing objections to the new genetics, we can see the beginnings of an appreciation for the work of field naturalists.

When Sumner examined the results of his survey in relation to evolution, he had to evaluate the biogeographical evidence that was dear to field workers but neglected by experimentalists. In particular, he wondered whether the distribution patterns of species studied by his survey provided any evidence for or against Jordan's views on the importance of isolation. Although he noted the differences between Jordan's evidence and his own materials, Sumner's first encounter with the work and evidence of the field naturalist led him to suspend judgment on one of the main criticisms of experimentalists: that specific differences could not be the result of natural selection (Sumner, Osburn, & Cole, 1913, pp. 187–188). More significantly, it also led him to accept field evidence such as the comparative study of distribution ranges. Sumner was beginning to cross the epistemological barrier between naturalists and experimentalists.

If Sumner's work at Woods Hole had warmed him to the kind of distributional evidence advocated by field naturalists, a change in his professional duties made him even more receptive to the work of field zoologists. In 1911, Sumner was appointed naturalist for the Bureau of Fisheries exploring vessel, the *Albatross.* He moved to the West Coast to work on a biological survey of the San Francisco Bay. While in this post for two years, he got to know the faculty of the Zoology Department at the University of California in Berkeley. This faculty included Grinnell, a champion of distribution studies who had built an institution to pursue that very kind of work.

After two years in California, Sumner submitted a "Proposed Plan for the Study of Certain Problems of Evolution and Heredity" to accompany his request for an appointment at the Scripps Institution. The plan focused on the heritability of subspecific characteristics. "Are the subspecies and geographical races of the systematic zoologists fixed, in the sense of being hereditary," Sumner asked. And, he continued, "if subspecific characteristics are really found to 'breed true,' do they owe their existence at the outset to 'mutations,' or to the cumulative effect of environmental influences, or to the mere fact of isolation, acting in some way independently of these influences?" It was Grinnell who a decade earlier had initiated a series of surveys in which he tried to gather distributional evidence against what he called the "notion of the evanescence of subspecific characters," common among "laboratory experimentalists" (Grinnell &

Swarth, 1913, pp. 394, 393). In what was reminiscent of Grinnell's papers, Sumner argued that California, given its great "range of environmental conditions . . . separated by geographical barriers" was a perfect place for his studies. More importantly, the materials already accumulated by Grinnell himself in the MVZ would provide the starting point for Sumner's research. This plan was to devote the first year to "museum studies," learning about mice taxonomy and distribution in the MVZ's rodent collections. From this first phase he would choose a particular group of mice. Then he would proceed to a second stage of "field observations and collecting." Only after these two stages did he plan to begin his breeding experiments.[22]

While waiting for his first experimental results, Sumner openly accepted distributional evidence. He began his experimental work by breeding several geographical races of deer mice (*Peromyscus*) from locations that differed in their meteorological conditions. The goal of these transplantation experiments was to investigate whether the morphological differences between the races were genetic or individually acquired. Given the early stage of his experimental work Sumner argued in his first report that he was "disposed to attach considerable importance to what have been called 'Nature's experiments.'" This was a direct reference to the distributional evidence cited by Grinnell (in his studies of California song sparrows) to argue for the heritable nature of subspecific differences.[23]

In the emerging collaboration between Sumner and Grinnell, the two naturalists had clearly distinct scientific identities. Sumner was the experimental biologist devising tests to decide between different explanations; Grinnell was the systematist with extensive field experience on wild populations and their ranges. Besides sharing his distributional evidence and giving him permission to use the MVZ's collections, Grinnell continuously provided Sumner with information regarding the logistics of fieldwork, including what traps to use, how to identify mice, and very detailed information as to itineraries and collecting places. Sumner instilled in Grinnell a certain appreciation for experimental work.[24]

In a period when name-calling was common among biologists who espoused different methods, such a relationship could only be built on profound mutual respect and the perceived existence of a common opposition. Institutional and intellectual isolation also helped. Sumner felt that geneticists did not take his work on *Peromyscus* seriously. Thus, he shared with the field naturalist Grinnell the feeling of being an outsider and having to defend continuously his line of work. For instance, on reading a paper by Grinnell that advocated the use of data from field observations, Sumner concurred: "That sort of thing, in my mind, is at least as good *genetics* as the great bulk of articles dealing with Mendelian 'unit factors.' I do not thereby mean to belittle your article." And, on receiving a copy of Grinnell's book on California game birds, Sumner ironically retorted, "As the volume concerns itself with neither Drosophila nor Oenothera, it is of course not *biology* in any proper sense, but as a contribution to *natural history* it is fine."[25]

In addition to having a common enemy, they felt they shared a common purpose for their work, despite the differences in approach. Sumner repeatedly asked Grinnell to join him on his field trips. Of course, the reason was partly that he could reap the benefits of having an experienced field companion next to him. But there was also the sense of a community of purpose underlying their differences in training and practice. They were studying the same evolutionary phenomena. "The points in question," argued Sumner, trying to convince Grinnell to tag along, "are just as vital to you as they are to me." The differences in their approaches, of course, necessitated slightly different modes of fieldwork ("differences in our technique, and possible resulting differences in field procedure"), as Sumner painstakingly pointed out. But, overall, they were two evolutionists working on the same general questions.[26]

Finally, Grinnell and Sumner continuously acted as sounding boards for the ideas each was considering separately. In this respect, their differences in scientific training and practice clearly represented an advantage. In order to reach beyond one's own discipline and communicate with a broader audience it was important to have a trusted colleague from outside one's own field. "I have read every word of your latest summary of the genetic situation," Grinnell wrote Sumner in 1917, "and the contentions were set forth so that even I got the ideas." Grinnell was more reluctant to set forth his general ideas on evolution on paper, feeling much more comfortable having them appear in the concluding sections of his many distributional articles. With Sumner's encouragement he finally published them in a paper entitled "Geography and Evolution."[27]

The existence of a common interest, which this relationship with Grinnell clearly exemplified, led Sumner to call for greater integration in biology. In 1927, when there was talk of disbanding the Western Society of Naturalists, he pleaded that such an action would be "a 'disgrace.'" There was an urgent need for "an organization devoted to the common meeting-ground of all students of the biological sciences," especially evolution, and without due attention to such common ground "the future of biology seems dark."[28]

Sumner understood the significance of his own personal contact with Grinnell and tried to bring together other field naturalists and geneticists. During a visit to Washington, DC, Sumner brought geneticists Sewall Wright and Leon Cole to the U.S. National Museum and had field zoologists from the Biological Survey show them some series of rodents from their collections. Sumner expected the geneticists to see with their own eyes the evidence collected by field workers, hoping that they would share his own open-mindedness toward nonexperimental work. Aware that he was expecting nothing less than a quasi-religious experience, he called this his "missionary work." The experiment left him pleasantly surprised and hopeful that other geneticists were becoming more open to consider what the systematists could offer.[29]

In the end, as he definitely abandoned his *Peromyscus* research in 1930, Sumner considered his own intellectual work a first step toward a synthesis. He understood this synthesis as a combination of fields and methods (taxonomy on one hand, genetics and biometry on the other) rather than one of ideas. In one of his last letters to Grinnell, Sumner remarked: "The synthesis of these fields which I have succeeded in making, in a feeble way, in my *Peromyscus* studies, and which [Harvey M.] Hall and some others are making with plants, is necessary to the sane development of both genetics and taxonomy."[30]

When the National Research Council's "Committee on Common Problems of Genetics and Paleontology" was established in the early 1940s, one of its first projects involved the "mutual education" of practitioners of both disciplines through their pairings as research partners (Cain, 2002). Acquiring a firsthand understanding of the modes of practice of biologists from other disciplines was seen as a necessary step by those seeking greater cooperation and synthesis. In the case of Grinnell and Sumner, we should perhaps speak of the "education of Francis Sumner." He was the one who was transformed the most by the experience, to the point that his identity was blurred and he came to be regarded as a systematist-mammalogist. When we look at those architects of the synthesis who bridged the gap between disciplines we see cases of field naturalists who either turned geneticists (Dobzhansky) or at least became very interested in genetics (Mayr). In Sumner we see the opposite process going on: an experimental evolutionist who came to value the scientific practice and evidence of field naturalists. He did this to such an extent that he merged the best from both traditions, and at the cost of being neglected by members of both sides. In this process, the collaboration of Joseph Grinnell should not be overlooked. Although they did not write papers together, Sumner and Grinnell certainly collaborated in several respects. They did fieldwork together, exchanged evidence and techniques, and acted as sounding boards for each other's ideas. This collaboration with a premier systematist certainly helped Sumner bridge the gap between genetics and systematics.

To summarize this section, I have examined two aspects of the synthesis that normally are overlooked. One concerns the contributions of turn-of-the-century field zoologists, especially as they developed methods that continued the tradition of field zoology in America and established institutions where later generations of students continued their work. The second kind of contribution is an early example of cooperation between a systematist (Joseph Grinnell) and a geneticist (Francis Sumner) in the 1910s and 1920s. The next section moves these elements forward to consider the case of Carl Hubbs. I present him as a systematist other than Mayr who made important contributions to the synthesis both in substance and in basic philosophy. I examine how he used an editorial position at *The American Naturalist* to advance his own views of the synthesis in his multiple roles as *evolutionist*, *systematist*, *American* systematist, and *ichthyologist*. The similarities and differences between Hubbs and Mayr are illuminating.

Hubbs as Reviews Editor in *The American Naturalist*

Beginning in 1941, Carl Hubbs edited a new "Reviews and Comments" section in *The American Naturalist*, devoted to reviewing new publications and relaying announcements of general interest to biologists. He focused on publications dealing with "the factors of organic evolution" and announcements of interest to "students of evolution." While crucial strides in the field of evolution were being made, but before the journal *Evolution* was established as the main outlet for evolutionary research, this forum was an excellent opportunity for a field zoologist to make his voice heard.

Hubbs advanced his own views on both the evolutionary process and the ways in which evolutionary integration and reform should be pursued. In doing so, he deployed a multilayered agenda. As a biologist interested in breaking the barrier between different biological disciplines, he emphasized the growing consensus on races and subspecies as steps in the speciation process, and advanced a selectionist and adaptationist point of view. As a field zoologist raised in the modern American school, he consistently emphasized the contributions of fellow field zoologists and the ecological aspects of speciation. Finally, as an ichthyologist, he was critical of some of the views on systematics that he associated with ornithologists in general, Mayr in particular.

Promoting integration of fields contributing to the evolutionary synthesis probably was Hubbs's main objective as a reviewer for the *Naturalist*, since his highest commendations went to works that brought together different disciplines and aimed for the generalist's point of view over that of the specialist. Huxley's *Evolution* was praised for its "masterly . . . synthesis of disciplines." Hubbs dubbed it "the outstanding evolutionary treatise of the decade, perhaps of the century" (Hubbs, 1943c, pp. 366, 365). Similar accolades went to Clausen, Keck, and Hiesey's "cooperative enterprise" (Hubbs, 1941a, p. 75). Works bringing together systematics and genetics, such as *The New Systematics* or the collaboration between Dobzhansky and Epling, were praised for "filling the chasms" splitting biology into systematics and genetics and into observation and experiment, and for organizing a "common front" in the study of evolution (Hubbs, 1945a, p. 76; Hubbs, 1941b, p. 176).

A defense of the emerging synthesis implied a strong criticism of those who deviated from the growing consensus, to the point that those who strayed from the new orthodoxy were subjected to the longest reviews. Hubbs repeatedly criticized Goldschmidt's views, calling them "almost Don Quixotic" and comparing them negatively to the positions advanced in *The New Systematics*. A particular target was Goldschmidt's "outstandingly fallacious" distinction between microevolution and macroevolution, which Hubbs attacked in several reviews (Hubbs, 1941c, pp. 272, 274; Hubbs, 1942b, 1945c). In addition to Goldschmidt, Hubbs also severely criticized the views of J. C. Willis, chastising him for ignoring the facts and interpretations of "modern evolutionary biology" (Hubbs, 1942a, p. 97).

In Hubbs's opinion, the emerging consensus was being reached because of two changes in the ways biologists looked at evolution. One involved overcoming "the hypercritical attitude of many biologists toward adaptation and selection" (Hubbs, 1941a, p. 77). Hubbs pointed out the adoption of an adaptationist and selectionist point of view as an advance among fellow field zoologists. The other central change was the increasing centrality of the phenomenon of speciation. Books rose or fell in Hubbs's estimation based on their treatment of speciation. Disciplines were more or less valuable depending on their contribution to the revelation of speciational processes. Even more than evolution, speciation seemed to be the "emergent science" (Hubbs, 1943a, p. 173).

Besides safeguarding the emerging consensus, an important part of Hubbs's agenda was to highlight the contributions of field zoologists, especially American zoologists from Joseph Grinnell's school. In a review of a posthumously published collection of Grinnell's papers Hubbs pointed out that "Grinnell consistently thought ahead of his time" (Hubbs, 1943d, p. 467). He also brought attention to works by some of Grinnell's students, such as Henry Fitch, Alden Miller, William Behle, and E. Raymond Hall (e.g., Hubbs, 1941d). All of these naturalists (as well as a few British field zoologists such as E. B. Worthington and David Lack) stressed one idea that Hubbs repeatedly expressed in his own works and correspondence: that the environmental aspects of speciation were as important as the genetic, or, as he liked to put it, "that the ecological potential may be more significant than the genetic" (Hubbs, 1947, p. 464). The role played by changes in the environment, and the ensuing variations in the availability of niches, were aspects of Grinnell's philosophy of speciation that Hubbs put at the core of his own. In his view, geneticists' emphasis on genetic mechanisms needed to be counterbalanced by an emphasis on ecology.[31]

The introduction of ecological aspects such as life histories, habits, and habitats into systematics was one of the positive steps taken by American field zoologists. Yet Hubbs considered fellow systematists to be lagging in their incorporation of statistical and experimental methods into their work. He highlighted Alden Miller's attempts at introducing statistical analysis and even some experiments into his systematic work. But other students of Grinnell, such as Hall and Behle, were criticized for not following in Miller's footsteps (Hubbs, 1942b, 1943b, 1946). The charge of giving slight attention to experimentation was leveled even on the contributors to *The New Systematics* and on Mayr himself (Hubbs, 1941b, 1943a). Hubbs's position was that experiment was a tool available to all biological disciplines, rather than being the prerogative of a few experimental disciplines within biology. Experimental systematics contributed to the integration of biology through the adoption of a common language with other disciplines. This integration was not merely an *entente* accomplished through a methodological division of labor between systematics and genetics.

The emphasis on ecology and on the need for experimental work in systematics usually accompanied Hubbs's attempts to differentiate his philosophy of speciation and systematics from that of ornithologists in general, and of Mayr in particular. In reviewing *Systematics and the Origin of Species*, Hubbs characterized Mayr's approach as "ornithocentric." Hubbs complained that the ichthyologists' ecological rules had been "inadequately presented." Mayr's extreme emphasis on geographical isolation had led him, in Hubbs's eyes, to relegate ecological and behavioral isolation to a secondary place.

In the end, the differences coalesced around their different attitudes toward the biological species concept. To Hubbs, this concept prevented experimental criteria from entering systematics, forcing "systematic procedure (and speciational considerations based thereon) into the realm of impression and authority" (Hubbs, 1943a, pp. 174, 173, 176; 1943e). If genetic isolation *in nature* was the criterion, experimental evidence was irrelevant. The biological species concept, the centerpiece of Mayr's philosophy of speciation and systematics, seemed to run against Hubbs's goal of making systematic criteria more objective (which was the basis of his strong defense of statistics and experiment in systematics).[32]

Hubbs's opposition to some of the views espoused by Mayr and other ornithologists is linked to his belief in the need for a plurality within systematics that would reflect the diversity of nature. This diversity, as exemplified by the differences between fishes and birds, precluded both the "old-line systematist" and the "modern speciationist" from adhering to one simple "correct" taxonomical system or one simple, fit-all theory of speciation. Yet the criteria had to be objective, and Hubbs perceived more objectivity in being a "damned morphologist" who used sophisticated statistical methods than in adopting a biological species concept that he understood to offer little functionality. "Systematics has been terribly burdened by subjective interpretations, and I think needs all the objectiveness that we can give it."[33]

Hubbs-the-evolutionist was certainly an ally of the architects of the synthesis. And Hubbs-the-systematist had goals in common with Mayr. But this should not preclude us from noticing the differences among systematists when it came down to specific issues, such as the significance of ecological factors or the acceptance of the biological species concept. Both Hubbs and Mayr accepted the main tenets of the emerging synthesis and participated actively in developing the infrastructure needed to establish evolutionary biology as a legitimate scientific discipline. But Hubbs was an American ichthyologist, and his views on these issues were bound to clash with those of old world ornithologists such as Mayr. Examining their diverse agendas will help us achieve a more complex view of the role of systematics during the synthesis.

Conclusion

This chapter complements recent advances in the historiography of the evolutionary synthesis by examining the role of members of the American community of field zoologists during 1900–1945. As experimental biologists abandoned the study of natural populations lured by the promise of mutationism and Mendelian genetics, field zoologists took the study of geographical variation and speciation as their own. At institutions like the MVZ at the University of California, Berkeley, and the University of Michigan Museum of Zoology, several generations of field zoologists transformed their tradition of fieldwork as they studied geographical distribution, variation, and speciation. The seeds planted by Joseph Grinnell and Charles C. Adams at the beginning of the century culminated in the work of Carl L. Hubbs, Lee R. Dice, Alden H. Miller, and others in the 1930s and 1940s.

The three cases or episodes that I have examined in this chapter are meant to complement existing lines of research on the synthesis period. These lines of research concern the emerging practices of evolutionary biology as well as the changing attitudes among different groups of evolutionists. My intention has been to offer counterpoints to some views that have emerged in the last decade regarding the relationship between field naturalists and experimentalists and the relationships among systematists.

For instance, a detailed examination of the changing practices of field biologists in the early decade of the twentieth century has begun with the recent work of Robert Kohler on what he calls the "border biology" of the 1930s and 1940s. He describes these practices as "traditional field methods amplified by numerical treatment systematically applied to natural units of population" (Kohler, 2002, p. 256). Comprehensive as his study is, not everyone will accept Kohler's view that the important thing about the practices of Mayr, Hubbs, and other field naturalists is their "lablike feel," their adherence to "laboratory standards of inference and proof."[34] In my opinion, we need to complement this view of field biological practices with an examination of how they emerged within specific schools and traditions of field practice, influenced by specific institutional settings. Although my analysis has only superficially delineated the institutional connections between several generations of field zoologists, I hope it offers a starting point for a complementary study of the historical dynamics of field practice that is more sensitive to its institutional context.

It is important to note that the contributions of field naturalists went beyond their specific research practices on geographical variation, isolation, and speciation. While most studies of the synthesis emphasize what systematists learned from geneticists, the case of Grinnell and Francis Sumner serves as a needed counterpoint. Here we find a field zoologist offering logistic and intellectual support to an experimental biologist. This relationship helped Sumner anticipate in the 1920s many of the preoccupations that participants in the synthesis tried to address more than a decade later. Among these were the need for common forums of discussion and for personal contact between practitioners of different disciplines, and an appreciation for the field naturalist's evidence and mode of practice.

Finally, I offer the case of Carl Hubbs's activities as reviewer for *The American Naturalist* as a complement to Mayr's omnipresence in studies of systematics in the synthesis. As with Mayr, Hubbs offers us a field zoologist using his position in a prominent public forum to facilitate the establishment of consensus, while publicizing the contributions of field zoologists to the emerging synthesis. But Hubbs's agenda included a defense of his own tradition of field studies, as well as an attack on the positions of other systematists, Mayr in particular. Thus, this case helps us appreciate the intellectual and institutional heterogeneity even within the community of evolutionary systematists that was beginning to coalesce in the 1940s.

A focus on the institutional settings where field zoologists conducted their work may shed some light on other aspects of the synthesis, such as the differences between Mayr and American systematists. Most avenues for employment for American field workers were related to conservation activities, such as state and federal fish commissions and natural resources departments. Naturalists such as Grinnell, Adams, and Hubbs worked for several of these institutions, which provided research funds as well as employment and publication opportunities. How did working for museums linked to state universities and conservation agencies compare to Mayr's position at the American Museum of Natural History? Did this difference in institutional affiliation among systematists influence their efforts to become active participants in the process of synthesis? These are some of the questions for further research that I hope to encourage with this chapter.

Acknowledgments

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Notes

1. Works examining the emergence of the synthesis include Provine (1978, 1979, 1986), Mayr and Provine (1980), Smocovitis (1992, 1994), Cain (1993, 1994, 2000a, 2000b, 2002), Adams (1994), and Ruse (1996).
2. Harwood (1993). A similar case can be made for the Soviet Union, as Adams (1968, 1970, 1980) has shown.
3. "Place modes" were understood to be the statistical characterization of the more common morphological traits for given geographical localities.
4. For examples of the field naturalists' reaction, see Anonymous (1894, 1898). Kohler (2002) examines biometry in the context of turn-of-the-century reform movements in biology.
5. Merriam to Henry F. Osborn, June 7, 1902, Reel 4, C. Hart Merriam Papers, Bancroft Library, University of California.
6. Report by Davenport on Eigenmann, November 18, 1904, Folder "Carl H. Eigenmann," Correspondence Collection, Carnegie Institution of Washington (hereafter, CHE-CIW). Eigenmann's original application was granted in 1903, but his application for renewal was turned down in January 1904. See "Abstract of Application, Grant #68," CHE-CIW.
7. Exchange between Eigenmann and Woodward, July–August 1906 and June 1908, CHE-CIW. Exchange between Eigenmann and Davenport, September–December 1909 and October 1911, in folder "Eigenmann, Carl H.," Charles B. Davenport Papers, American Philosophical Society Library.

8. On the general reception of de Vries's work, see Allen (1969). For the analysis of a specific case that complements Allen's view, see Kingsland (1991).
9. Magnus (1989) discussed the isolation debate generally.
10. Adams, "Some General Principles of Animal Ecology," unpublished manuscript, Box 28, Charles C. Adams Collection, Western Michigan University Archives and Regional History Collections.
11. On Adams, see Ilerbaig (1999).
12. Adams to G. A. Hinnen (Secretary, Cincinnati Society of Natural History), January 27, 1906, Box 18-II, Charles C. Adams Collection, Western Michigan University Archives and Regional History Collections.
13. For biographical information on Grinnell, see Grinnell (1940) and Miller (1964). See also folders "Written examination for Ph.D., Spring 1913," and "Tribute to Profs. Gilbert & Price," Carton 3, Joseph Grinnell Papers (Additions), Bancroft Library, University of California.
14. See Star and Griesemer (1989) and Griesemer (1990).
15. Ilerbaig (1999) examines Shelford's and Adams's problems in making ecology a legitimate science. Kohler (2002) offers another view on this general issue.
16. For instance, Mayr wrote of "Sumner and Dice and their school" (Mayr, 1980b, p. 132).
17. For examples of Dice's work and views on distribution at this stage, see Dice (1922a, and 1922b). Lee R. Dice to J. C. Merriam, December 10, 1921; F. E. Clements to Merriam, December 14, 1921; Merriam to Dice, December 19, 1921; [Lee R. Dice], "A Preliminary Classification of the Biotic Areas of the United States," Folder "Lee R. Dice," Correspondence Collection, Carnegie Institution of Washington (hereafter, LRD-CIW).
18. See Dice to Merriam, May 5, 1926, and "Studies of the Factors Determining Speciation in Mammals and Reptiles (By the Carnegie Institution of Washington and the Museum of Zoology, University of Michigan)," LRD-CIW. Merriam had advised Dice to get in touch with Clements and the personnel at the Desert Laboratory when he turned down Dice's earlier proposal.
19. Dobzhansky to Hubbs, July 22, 1937, folder "Speciation, General, 1935–1940," box 35, Carl Hubbs Papers, Scripps Institution of Oceanography Archives (SIO). The papers of the two symposia were published in successive issues of *The American Naturalist, 74* (1940), 193–278, 189–321. Dice delivered a paper in each of the symposia.
20. Sumner to Jordan, July 30, 1923, box 108, folder 935, David Starr Jordan Papers, Stanford University Libraries Archives.
21. Sumner to William Emerson Ritter, February 1, 1913, quoted by Provine (1979, pp. 219–220).
22. Francis Sumner, "Proposed Plan for the Study of Certain Problems of Evolution and Heredity," [April 1913?], copy in folder "Sumner, Francis 1914–1917," Correspondence Files, Museum of Vertebrate Zoology, University of California, Berkeley (hereafter, MVZ-Sumner, followed by the folder years).
23. Sumner (1915, pp. 696–697). In correspondence with Grinnell, Sumner referred to this evidence as "your dope." Sumner to Grinnell, September 2, 1914, MVZ-Sumner 1914–1917.
24. They frequently joked about these differences in training and scientific practice. For instance, when Grinnell argued in one of his papers that "a little experimentation would go far to proving" whether typical desert animals could cross water barriers, Sumner retorted: "Welcome into the camp of the experimentalists! What is the scriptural quotation about the sinner that repenteth? Verily, the heaven is working." Sumner to Grinnell, March 28, 1914, MVZ-Sumner 1914–1917. And when Grinnell asked for suggestions for keeping mice alive, since one of the students in Berkeley was trying to do experimental work, Sumner concluded (after offering the appropriate information), "Good work! Biology is the science of *life*, not of dead skins seasoned with arsenic. (A rejoinder is expected)." Sumner to Grinnell, November 16, 1916, MVZ-Sumner 1914–1917.

25. Sumner to Grinnell, undated [January or February 1917], MVZ-Sumner 1914–17. The article Sumner referred to was Grinnell (1917). Sumner to Grinnell, March 7, 1919, MVZ-Sumner 1918–1921.
26. Sumner to Grinnell, March 12, 1916, MVZ-Sumner 1914–1917. Sumner to Grinnell, undated [received March 11, 1920], MVZ-Sumner 1918–1921.
27. Grinnell to Sumner, November 5, 1917, MVZ-Sumner 1914–1917. Sumner to Grinnell, October 9, 1923, MVZ-Sumner 1923–1926. The paper (Grinnell, 1924) was delivered at the joint meeting of the Western Society of Naturalists and the Ecological Society of America in 1923.
28. Sumner to C. O. Esterly, March 5, 1927, copy in MVZ-Sumner 1927–1931. See also Sumner to Tracy Storer, November 8, 1921, MVZ-Sumner 1918–1921.
29. Sumner to Grinnell, January 6, 1924, MVZ-Sumner 1923–1926.
30. Sumner to Grinnell, December 1, 1930, MVZ-Sumner 1927–1931.
31. About one third of the evolution-related works reviewed by Hubbs between 1941 and 1947 were authored by Grinnell or his students. See also Hubbs (1940, p. 198; 1955, pp. 5–6) and Hubbs to David H. Thompson, August 25, 1936, folder "Speciation, General, 1935–1940," box 35, Carl Hubbs Papers, SIO for similar articulations of this idea.
32. The criticism of reintroducing authority and impression into the practice of systematics was extended to other ornithologists. See Hubbs (1945b, p. 277).
33. See Hubbs's contribution to *Criteria for Vertebrate Subspecies, Species, and Genera*. Hubbs to Carl Epling, December 28, 1943, folder "Speciation, General, 1941–1943," box 35, Hubbs Papers, SIO.
34. Kohler (2002, pp. 264, 265). Similar references to the adoption of the ideals and modes of thinking of laboratory science by field naturalists abound throughout Kohler's book.

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