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The Equally Wonderful Field: Ernst Mayr and Organismic Biology

ABSTRACT

Biologists in the 1960s witnessed a period of intense intra-disciplinary negotiations, especially the positioning of organismic biologists relative to molecular biologists. The perceived valorization of the physical sciences by "molecular" biologists became a catalyst creating a unified front of "organismic" biology that incorporated not just evolutionary biologists, but also students of animal behavior, ecology, systematics, botany—in short, almost any biological community that predominantly conducted their research in the field or museum and whose practitioners felt the pinch of the prestige and funding accruing to molecular biologists and biochemists. Ernst Mayr, Theodosius Dobzhansky, and George Gaylord Simpson took leading roles in defending alternatives to what they categorized as the mechanistic approach of chemistry and physics applied to living systems—the "equally wonderful field of organismic biology." Thus, it was through increasingly tense relations with molecular biology that organismic biologists cohered into a distinct community, with their own philosophical grounding, institutional security, and historical identity. Because this identity was based in large part on a fundamental rejection of the physical sciences as a desirable model within biology, organismic biologists succeeded in protecting the future of their field by emphasizing the deep divisions that ran through the biological sciences as a whole.

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The following abbreviations are used: CDP, Cyril Dean Darlington Papers, CSAC 106.3.85, Special Collections and Western Manuscripts, Bodleian Library, University of Oxford, Oxford, UK; CES, papers related to the Conference on the Evolutionary Synthesis, Ernst Mayr Papers, B M541, American Philosophical Society, Philadelphia, PA; EMP, Ernst Mayr Papers, Faculty Papers, Harvard University Archives, Pusey Library, Harvard University, Cambridge, MA; GSP, George Gaylord Simpson Papers, MS Coll. 31, American Philosophical Society, Philadelphia, PA; HUGFP, Harvard University, Biography, Faculty Papers; NAS, National Academy of Sciences; NIH, National Institutes of Health; NMS, National Medal of Science; NSF, National Science Foundation; TDP, Theodosius Grigorievich Dobzhansky Papers, B D65, American Philosophical Society, Philadelphia, PA.

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During the 1960s, in reaction to the increasing prestige of biochemistry and molecular biology, biologists who studied the systematics of animals and plants, animal behavior, ecology, and evolution began to band together under a new name: organismic biology. Although the term had been in infrequent use since at least the 1930s, it became a touchstone for biologists only after Ernest Nagel's 1961 *Structure of Science*, in which he spent a chapter unfavorably contrasting "organismic" biology with "mechanistic" biology.[1] Nagel insisted that although the reduction of organismic biology to physico-chemical laws had not yet been accomplished, the question of whether it *could* was empirical. There was no necessary philosophical or biological justification he could see for maintaining biological knowledge as distinct from the sciences of nonliving substances. Biologists like Ernst Mayr, who believed that *true* biology could never be explained using solely physical and chemical approaches, vilified Nagel's position, but embraced his terminology.[2]

For organismic biologists, the 1960s began with the 1959 Centennial Celebration of Darwin's publication of *On the Origin of Species*.[3] For Ernst Mayr, history provided a way to investigate the intellectual antecedents of his own approach to evolution and systematics. In part through Mayr's patronage, the history of evolutionary theory offered historians of science an opportunity to interact with many of the great names in the field and an attractive alternative

1. Ernest Nagel, *The Structure of Science: Problems in the Logic of Scientific Explanation* (New York: Harcourt, Brace & World, 1961), chapt. 12, "Mechanistic Explanation and Organismic Biology." Nagel's chapter was a revised version of an earlier paper that based on citation analysis seems to have attracted far less attention from biologists: Ernest Nagel, "Mechanistic Explanation and Organismic Biology," *Philosophy and Phenomenological Research* 11, no. 3 (1951): 327–38.

2. Ernst Mayr, "Cause and Effect in Biology: Kinds of Causes, Predictability, and Teleology Are Viewed by a Practicing Biologist," *Science* 134 (1961): 1501–06; Ernest Caspari, "Introductory Remarks," *The American Naturalist* 97, no. 896 (1963): 261–63; Theodosius Dobzhansky, "Biology, Molecular and Organismic," *American Zoologist* 4 (1964): 443–52. Later philosophers have illustrated how Nagel's valorization of reductionism in science does not work even within the field of genetics; see Philip Kitcher, "1953 and All That: A Tale of Two Sciences," *Philosophical Review* 93, no. 3 (1984): 335–73.

3. Vassiliki Betty Smocovitis, "The 1959 Darwin Centennial Celebration in America," *Osiris* 14 (1999): 274–323; Sol Tax, ed., *Evolution After Darwin: The University of Chicago Centennial* (Chicago: University of Chicago Press, 1960), Vol. 1, *The Evolution of Life*, Vol. 2, *The Evolution of Man*, Vol. 3, *Issues in Evolution* (ed. Sol Tax and Charles Callender).

to the then-dominant history of the physical sciences.[4] Mayr delighted in spending time with historians and philosophers of biology and encouraging them in their work—especially if it dealt with the history or philosophy of evolution and not mechanistic science.

For molecular biologists, on the other hand, the early 1960s were filled with news about the race to break the genetic code, and Nobel Prizes for the discovery of the structure of DNA.[5] During the 1960s, tensions within the biological sciences increased dramatically, as members of distinct approaches to the study of the living world vied for pieces of the rapidly increasing monies available to fund research from the National Science Foundation, the National Institutes of Health, and other federal agencies.[6] Although molecular biologists and biochemists may have seen each other as primary rivals in this fight, naturalists of all sorts began to worry about the future of the biological study they knew and loved as media attention, Nobel Prizes, institutional positions, and funding were heaped upon biochemists, molecular biologists, cellular biologists, and even biophysicists.[7]

4. See, for example, Smocovitis' description of Mayr's pervasive influence in "Ernst Mayr (1904–2005), Darwin of the 20th Century, Defender of the Faith," *Biological Theory* 2, no. 4 (2007): 409–12; Michael Ruse, "Obituary: Ernst Mayr, 1904–2005," *Biology and Philosophy* 20 (2005): 623–31; Jürgen Haffer, *Ornithology, Evolution, and Philosophy: The Life and Science of Ernst Mayr* (New York: Springer, 2009); and Mary Winsor, "Ernst Mayr, 1904–2005," *Isis* 96 (2005): 415–18.

5. On the important role commemorations played in establishing the history of molecular biology, see Pnina Abir-Am, "Essay Review: How Scientists View Their Heroes: Some Remarks on the Mechanism of Myth Construction," *Journal of the History of Biology* 15, no. 2 (1982): 281–315; Pnina Abir-Am, "The First American and French Commemorations in Molecular Biology: From Collective Memory to Comparative History," *Osiris* 14 (1999): 324–70; Soraya de Chadarevian, *Designs for Life: Molecular Biology after World War II* (Cambridge: Cambridge University Press, 2002), 166–70. De Chadarevian and Abir-Am note that by the mid-1960s, the place of the discovery of the structure of DNA in the history of molecular biology was largely secure, even if the reasons for its centrality remained contested.

By the 1970s, even *National Geographic Magazine* (known for its interest in promoting field-based biological endeavors) published a series of articles together entitled "The New Biology"—Rick Gore, "The Awesome Worlds Within a Cell," *National Geographic Magazine* 150, no. 3 (1976): 354–95; Robert F. Weaver, "The Cancer Puzzle," *National Geographic Magazine* 150, no. 3 (1976): 396–99; Rick Gore, "Seven Giants Who Led the Way," *National Geographic Magazine* 150, no. 3 (1976): 400–07. The seven giants they picked were Anton van Leeuwenhoek, Charles Darwin, Gregor Mendel, Louis Pasteur, Thomas Hunt Morgan, James D. Watson, and Francis Crick.

6. Toby Appel, *Shaping Biology: The National Science Foundation and American Biological Research, 1945–1975* (Baltimore: Johns Hopkins University Press, 2000).

7. On the discovery of the structure of DNA, the race to break the genetic code, and the relationship between biochemistry and molecular biology, see, for example, Pnina Abir-Am, "The

In reaction, botanists, zoologists, taxonomists, and ecologists who studied the whole plant or whole animal defined themselves in opposition to those scientists who studied biological organization on a sub-organismal scale. They came to deemphasize (but not forget) the traditional taxonomic boundaries between their fields and together advocated an *organismic* or *organismal* approach to the study of life.[8] Whereas molecular biologists worked valiantly to find practical applications of their research for human medical conditions, organismic biologists also sought to claim the human as part of their jurisdiction. Yet rather than concentrating on medicine, they suggested that organismic biology could shed light on the human condition, through an evolutionary lens.

The cast of characters for this paper consists of those self-defined organismal biologists who invested themselves in maintaining the boundaries of their field in the 1960s: Ernst Mayr (to whom I devote particular attention), Theodosius Dobzhansky, and George Gaylord Simpson, all of whom were already iconic figures in evolutionary theory. This paper explores their role in producing philosophical and historical accounts of organismic biology that served to demarcate their endeavors from those of molecular biologists. Yet as many historians have vividly illustrated, evolutionary biologists in the 1960s disagreed over just about every major question they posed to one another, including the unit of selection, the mechanisms by which natural selection acted, the importance of mathematical models, and the applicability of *Drosophila*

Politics of Macromolecules: Molecular Biologists, Biochemists, and Rhetoric," *Osiris* 7 (1992): 164–91; Pnina Abir-Am, "The Molecular Transformation of Twentieth-Century Biology," in *Science in the Twentieth-Century*, ed. John Krige and Dominique Pestre (Amsterdam: Harwood Academic, 1997): 495–524; de Chadarevian, *Designs for Life* (ref. 5); Soraya de Chadarevian and Jean-Paul Gaudillière, eds., "The Tools of the Discipline: Biochemists and Molecular Biologists," special issue of the *Journal of the History of Biology* 29, no. 3 (1996); Michel Morange, *A History of Molecular Biology* (Cambridge, MA: Harvard University Press, 1992); Angela Creager, *The Life of a Virus: Tobacco Mosaic Virus as an Experimental Model, 1930–1965* (Chicago: University of Chicago Press, 2002); Lily Kay, *The Molecular Vision of Life* (Oxford: Oxford University Press, 1993); Lily Kay, *Who Wrote the Book of Life? A History of the Genetic Code* (Palo Alto, CA: Stanford University Press, 2000); Frederic L. Holmes, *Meselson, Stahl, and the Replication of DNA: A History of the Most Beautiful Experiment in Biology* (New Haven: Yale University Press, 2002); Robert C. Olby, *The Path to the Double Helix* (Seattle: University of Washington Press, 1974); Hans-Jörg Rheinberger, "Recent Science and Its Exploration: The Case of Molecular Biology," *Studies in History and Philosophy of Biological and Biomedical Sciences* 40, no. 1 (2009): 6–12.

8. At first, "organismic" biology distinguished between the two kinds of biological investigation I elucidate here, and "organismal" biology referred to research at the level of the organism (as opposed to either populations or cells). In later usage the two words become almost synonymous, with "organismal" biology coming to stand for all kinds of biological research at the organismal level, or higher.

research to understanding evolutionary processes in nature.[9] When it came to defending organismic biology, the strategies of Mayr, Dobzhansky, and Simpson were equally diverse.

The perceived valorization of the physical sciences by "molecular" biologists became a catalyst creating a unified defensive front of "organismic" biology that incorporated not just evolutionary biologists, but also students of animal behavior, ecology, systematics, botany—in short, almost any biological discipline that was predominantly practiced in the field or museum and whose practitioners felt the pinch of the prestige and funding accruing to molecular biologists.[10] The term "molecular" biology, in this context, reflects the usage of organismic biologists at the time, when it was intended as a catchall phrase identifying sub-organismic approaches to the study of life. This usage differs dramatically from that of scientists who self-identified as molecular biologists, using the term instead to distinguish themselves from biochemists, for example. Although the origins of such a divide within biology were certainly in place by the 1950s, it was through the increasingly tense relations with molecular biologists in the 1960s that "organismic" biologists cohered into a distinct community.[11] Organismic biologists created their own philosophical grounding (conceptions of causality), historical identity, and claims to unique forms of knowledge (the evolution of human nature), based in large part on a fundamental rejection of the physical sciences as a desirable model within biology.[12]

This paper addresses three problems that organismic biologists believed were in need of solutions in order to succeed in their struggle with the molecular biologists: Were ideas of reductionism and causation developed in the physical sciences applicable to biological research? Should organismic and molecular

9. Dietrich, for example, has suggested that even as early as the 1940s one of the only things about which the architects of the modern synthesis could agree was that developmental biologist Richard Goldschmidt could be identified as a common enemy. Michael Dietrich, "Richard Goldschmidt's 'Heresies' and the Evolutionary Synthesis," *Journal of the History of Biology* 28, no. 3 (1995): 431–61.

10. Theodosius Dobzhansky, "Are Naturalists Old-Fashioned?" *American Naturalist* 100, no. 915, Special One Hundredth Anniversary Year Issue (1966): 541–50.

11. Joseph Allen Cain, "Ernst Mayr as Community Architect: Launching the Society for the Study of Evolution and the Journal *Evolution*," *Biology and Philosophy* 9 (1994): 387–427; Vassiliki Betty Smocovitis, "Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology," *Journal of the History of Biology* 25, no. 1 (1992): 1–65 (see esp. 58–60); Ernst Mayr, "Where Are We?" *Cold Spring Harbor Symposium on Quantitative Biology* 24 (1959): 1–14.

12. The idea of co-production has a large historiography within the science and technology studies literature and environmental history. Notably, see Sheila Jasanoff, ed., *States of Knowledge: The Co-Production of Science and the Social Order* (New York: Routledge, 2004).

biology be recognized as independent enterprises at an institutional level? Which approaches to nature were historically responsible for the great advances of twentieth-century evolutionary thought? For organismic biologists, these institutional negotiations, modes of explanation, and claims for historical foundations all came to define what they saw as two distinct approaches to biological research.

I argue that the boundary between molecular and organismic biology was erected and maintained by organismic biologists in an attempt to protect their approach to the life sciences from any further encroachment by the physical sciences.[13] Their success was so great, I believe, that it has left historians of biology with the distinct impression that organismic biology has always existed, albeit under names like natural history or evolutionary biology. Which in one sense it has—biologists have been studying whole organisms for centuries—but in another sense, organismic biology in the 1960s represented a new set of coalitions and professional associations, a re-sorting of allegiances within the biological sciences, defined by the politics inherent to biological research at that historical moment.[14] The struggle for unity in the 1940s had given way to a contest for authority by the 1960s.[15] As a community, organismic biologists

13. It seems likely that the deeply felt urgency of organismal biologists to maintain distinct divisions within the biological sciences was not as commonly felt among molecular biologists. In a revealing anecdote, Lindley Darden remembers a conversation she had with Matthew Meselson, in which she asked him if he called himself a "molecular biologist." He said he preferred "biologist" because he had always had an interest in evolution (Lindley Darden, personal communication).

14. Spencer Weart has described a similar kind of defensive consolidation of widely differing specialties into the solid-state physics community in the 1950s, as a function of the continued diversification of sub-disciplines of physics in the first half of the twentieth century. He contrasts this with a more typical narrative of how a scientific community develops in time—like ivy growing on a wall, there are a few initial key papers that slowly grow into a full-fledged vine/community. In this way, the histories of solid-state physics and organismal biology are quite similar. Where they diverge is through the simultaneous development of formal designations of a "discipline" in solid-state physics (university chairs, conferences, journals, etc.) that don't identify organismal biology as a distinct sub-discipline in the 1960s. One might argue that pre-existing journals, such as *Evolution* and *American Naturalist*, could have performed such a function, but these journals continued to restrict their publications to different subsets of the organismal community. Spencer Weart, "The Solid Community," in *Out of the Crystal Maze: Chapters from the History of Solid State Physics* (Oxford: Oxford University Press, 1992), 617–69; David Kaiser, "Information Overload," in *American Physics and the Cold War Bubble* (Chicago: University of Chicago Press, forthcoming).

15. Recent books on the history of the synthesis period include Joseph Allen Cain and Michael Ruse, eds., *Descended from Darwin: Insights into the History of Evolutionary Studies, 1900–1970* (Philadelphia, PA: American Philosophical Society, Transactions of the American Philosophical

succeeded in their goal of securing their philosophical, institutional, and historical position in the biological sciences, but at the cost of highlighting deep divisions within the biological sciences.

PROBLEM ONE, MODES OF EXPLANATION IN BIOLOGY

Methods for dividing biological research into multiple modes of inquiry based on level of biological organization were certainly in place by the 1950s. Over the course of the 1960s, however, increasing tensions between molecular (sub-organismal) and organismic (organismal and super-organismal) biologists seemed to suggest that the division around *organism* mattered far more than differences surrounding any of the other organizational levels. It was during this decade that Mayr, Simpson, and Dobzhansky came to defend the dividing line between organismic and molecular biology as distinguishing true (i.e., evolutionary) biology from mere chemical and physical investigations of its molecules.

In the 1950s, geneticist Sewall Wright published two articles that developed the idea of a hierarchy of biological sciences arranged according to levels of biological organization.[16] He took his cue from a combination of cell theory (organisms are a tightly knit colony composed of other organisms) and Alfred Emerson's idea of communities as superorganisms (a species is a single, loosely knit organism composed of individuals).[17] Wright suggested each level of

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Society, vol. 99, part 1, 2009); Jean Gayon, *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Natural Selection* (Cambridge: Cambridge University Press, 1998), and Vassiliki Betty Smocovitis, *Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology* (Princeton: Princeton University Press, 1996). Smocovitis's *Unifying Biology* includes an extensive bibliography of historical research on the evolutionary synthesis and reviews the diverse array of historical interpretations of the synthesis period. On my use of the term "synthesis period" see Joe Cain, "Rethinking the Synthesis Period in Evolutionary Studies," *Journal of the History of Biology* 49 (2009): 621–48.

16. Of great use to me as I worked through this section were John Beatty, "Evolutionary Anti-Reductionism: Historical Reflections," *Biology and Philosophy* 5 (1990): 199–210; Smocovitis, "Unifying Biology" (ref. 11), 57–60; Smocovitis, *Unifying Biology* (ref. 15), 174–78.

17. Sewall Wright, "Gene and Organism," *The American Naturalist* 87, no. 832 (1953): 5–18. Gregg Mitman's *State of Nature: Ecology, Community, and American Social Thought, 1900–1950* (Chicago: University of Chicago Press, 1992) explicates the importance of conversations about "levels" of biological organization to the biological sciences in the first half of the twentieth century. By the second half of the twentieth century, seeing communities as superorganisms was in decline, but the rhetoric of "levels" of biological organization and investigation continued

biological organization was capable of growth and reproduction, and possessed "characteristics that are more than those of a mere aggregation of similar individuals."[18] Wright then extended this idea to a hierarchy of the biological sciences based on the level of biological organization under investigation.[19] Of great significance to Wright was the fact that geneticists, of many different stripes, had contributed crucial information to the understanding of most levels of biological organization (populations, multicellular organisms, cells, and molecules. (Fig. 1) The genes themselves he compared to "complex creatures" remarkably similar to the living individuals that had inspired natural historians like entomologist William Morton Wheeler.[20] By way of conclusion, Wright argued that genetics would only cease to exist as a field if all biological theory became completely united through its efforts. Genetics, he continued, "played a major role in binding all [biological] science into one coherent whole."[21]

Mayr's response came surely (if not swiftly). Mayr had been worried about the influence of reductionist biology since at least 1949, when he wrote to a friend that despite his affection for the American Museum of Natural History where he worked, he was tempted to find a university position that involved teaching because he felt that "in most places they do everything to discourage young taxonomists rather than the opposite . . . I feel that it is very necessary to provide some counterbalance against the strictly physiological, bio-chemical

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apace. Wright, Warder Clyde Allee, and Emerson were colleagues at the University of Chicago, and it is easy to see the influence of Allee and Emerson on Wright's thinking. Wright cites, for example, Alfred Emerson, "Social Coordination and the Superorganism," *American Midland Naturalist* 21 (1939): 182–209, and R. W. Gerard, "Organism, Society and Science," *Scientific Monthly* 50 (1940): 340–50, 403–12, 530–35. On the superorganism as a concept, see also William Morton Wheeler, "The Ant Colony as an Organism," *Journal of Morphology* 22, no. 2 (1911): 307–25, and on biological levels of analysis, see Alex B. Novikoff, "The Concept of Integrative Levels and Biology," *Science* 101, no. 2618 (1945): 209–15.

18. Wright, "Gene and Organism" (ref. 17), 6.

19. Sewall Wright, "Genetics and the Hierarchy," *Science* 130, no. 3381 (1959): 959–65.

20. Wright cites Wheeler's "The Dry-Rot of Our Academic Biology," *Science* 57, no. 1464 (1923): 61–71, in which Wheeler exhorts naturalists to look up from their desks and books to enjoy being in nature with the animals they study. Wheeler, trained as a developmental biologist, later came to ironically characterize himself as a rustic entomologist. Abigail J. Lustig, "Ants and the Nature of Nature in Auguste Forel, Erich Wasmann, and William Morton Wheeler," in *The Moral Authority of Nature*, ed. Lorraine Daston and Fernando Vidal (Chicago: University of Chicago Press, 2004), 282–307.

21. Wright, "Genetics and the Hierarchy" (ref. 19), 965.

Biological level		Climax phase: Description	Climax phase: Dynamics	History: Description	History: Dynamics	Multiplication
Ecologic system	World biota	Bio-geography	Biotic stability	Paleontology	Biotic evolution	
	Local biota	Ecology (community)		Ecologic succession		
Interbreeding population	Species	Taxonomy	Species stability	Phylogeny	Macro-evolution Trans-formation	Species cleavage
	Deme	Demography	(7) *Population genetics*		Micro-evolution (7) *Population genetics*	
Multicellular organism	Individual	External characters	Behavior (6) *Genetics of behavior*	Life history		Physiology of reproduction (1) *Formal genetics*
	Organ	Anatomy	Gross physiology	Descriptive embryology	Morphogenesis (5) *Developmental genetics* Histogenesis	
	Tissue	Histology				
Cell	Cytoplasm and nucleus	Cytology	General physiology (4) *Physiological genetics*	(2) *Cytogenetics*		Mitosis
Autonomous macro-molecule	Gene	(3) *Theory of the gene*		*Gene mutation*		
	DNA	*Gene chemistry*	*Gene physiology*	*Description*	*Process*	*Gene duplication*
Nonautonomous molecule		Biochemistry				

FIG. 1 Sewall Wright's 1959 Hierarchy of the Biological Sciences. Note that the various fields of genetics are present at every level except the largest, ecologic system, and the smallest, nonautonomous molecule. An earlier iteration of this figure appeared in Wright's "Gene and Organism," *The American Naturalist* 87, no. 832 (1953): 5–18, on 10. *Source*: Sewall Wright, "Genetics and the Hierarchy of Biological Sciences," *Science* 130, no. 3381 (1959): 962. Reprinted with permission of AAAS.

trend in our zoology departments."[22] Mayr took the opportunity of his 1959 introductory address to the annual Cold Spring Harbor Symposium on Quantitative Biology to insist on the confusion between evolutionary and genetic perspectives in the existing literature on the history of biology.[23] In his paper, he did not react to Wright directly, but instead to what he perceived as a groundswell in molecular biologists' claims to be "modern" biologists in comparison to "classical" or "old-fashioned" natural historians.[24] The topic of the symposium was "Genetics and Twentieth Century Darwinism" in honor of the one hundredth anniversary of Darwin's *On the Origin of Species*. Mayr contended that "virtually all the early Mendelians" were rabidly anti-selectionist, preferring to explain evolutionary change in terms of mutations. Only the simultaneous downfall of DeVriesian saltationism and Lamarckian inheritance of acquired characteristics had made possible the evolutionary synthesis of genetics and evolutionary theory in the 1930s. In Mayr's recounting, historical claims that the mathematical-genetical theories of Ronald Fisher, J. B. S. Haldane, and Sewall Wright formed the basis of the evolutionary synthesis were sadly mistaken.[25] In fact, he argued, geneticists of the early twentieth century *delayed* the synthesis. Like Wright, Mayr next broke modern biological research into five distinct "levels of integration"—namely, "the chromosome, the individual, the population, the species, and the phyletic line."[26] He discussed each in turn, highlighting the unanswered evolutionary questions each level of integration posed to the biologists seated in front of him. Evolutionary biology was not

22. Ernst Mayr to Erwin Stresemann, 8 Aug 1949, quoted in Haffer, *Ornithology, Evolution, and Philosophy* (ref. 4), 260.

23. Simpson also used the occasion of the Darwin Centennial to advance the cause of organismal biology. Mayr, "Where Are We?" (ref. 11); George Gaylord Simpson, "The World into Which Darwin Led Us," *Science* 131, no. 3405 (1960): 966–74; Smocovitis, "1959 Darwin Centennial Celebration" (ref. 3).

24. William Provine has also noted how Mayr was not the first organismal biologist to react to such claims by geneticists; Conrad Waddington took up a defensive shield earlier in the 1950s. William Provine, *Sewall Wright and Evolutionary Biology* (Chicago: University of Chicago Press, 1989), 480–84; Ernst Mayr and William Provine, eds., *The Evolutionary Synthesis: Perspectives on the Unification of Biology* (Cambridge, MA: Harvard University Press, 1980), "Epilogue," 401–03; Conrad Hal Waddington, "Epigenetics and Evolution," *Symposia of the Society for Experimental Biology* 7 (1953): 186–99; idem, *The Strategy of the Genes: A Discussion of Some Aspects of Theoretical Biology* (London: Allen and Unwin, 1957), 59.

25. Ronald Fisher, *The Genetical Theory of Natural Selection* (Oxford: Clarendon Press, 1930); J. B. S. Haldane, *The Causes of Evolution* (London: Longman, Green and Company, 1932); Sewall Wright, "Evolution in Mendelian Populations," *Genetics* 16 (1931): 97–159.

26. Mayr, "Where Are We?" (ref. 11), 8.

finished but deserved equal respect and footing with molecular biology. Indeed, biologists ignored or belittled evolutionary theory at their own peril—at stake was not only an understanding of their universe, but the very future of man, as I will discuss shortly.

Although Mayr keenly felt the division between two different kinds of biological investigation, he had not yet settled on a consistent terminological convention by which to refer to them. Neither he nor Wright yet used the words *organismic* or *molecular* as shorthand for this incommensurability. In part, this stems from the fact that in 1959 Mayr was more interested in defending evolution against the influence of geneticists than he was in defending the broader community of organismic biologists against molecular biology. This would slowly change, although these two defensive lines can be difficult to tease apart because they were engaged in the same battle to maintain the position of museum- and field-based biology in a rapidly changing world.

In 1961, Mayr published a direct challenge to Nagel's philosophical assertions and one possible reading of Wright's organizational scheme—biologists could not understand life simply by studying its molecules.[27] He began the paper by contrasting his perspective with that of the "logician" Nagel, whom he had recently heard speak at the nearby Massachusetts Institute of Technology's Hayden Lecture series.[28] Echoing his earlier concerns, Mayr argued that *functional* and *evolutionary* approaches to biological research (Nagel's mechanistic and organismic approaches) presupposed two different kinds of causal questions, which he termed proximate and ultimate causes.[29] Mayr defined functional biology as the quest to understand the inner physiological workings of organisms isolated from the complexities of the organism as a whole. Functional biologists, he continued, asked *how* biological phenomena were produced, and sought immediate mechanistic causes, and he consistently referred to molecular biology in his examples. Evolutionary biologists, on the other hand, who kept organisms (either individual or species) as their focus of study, sought to answer *why* or *how come* biological phenomena were produced

27. Mayr, "Cause and Effect in Biology" (ref. 2), 1501.

28. Ibid., 1506.

29. John Beatty, "The Proximate/Ultimate Distinction in the Multiple Careers of Ernst Mayr," *Biology and Philosophy* 9 (1994): 333–56. Beatty illustrates how Mayr continued to reconstitute his proximate-ultimate distinction to address new foes of the neo-Darwinian paradigm, including developmental biology in the 1980s. See also Thomas Junker, "Ernst Mayr (1904–2005) and the New Philosophy of Biology," *Journal for General Philosophy of Science* 38 (2007): 1–17.

in an organism.[30] The answer to these questions involved understanding the evolutionary past of the organism, the ecological environment in which the organism lived, and any genetic predispositions in the organism. Mayr differentiated between what he saw as mechanistic, molecular approaches and truly biological approaches to the study of life, which required an evolutionary perspective and the study of organisms. Even though Mayr had first conceived of the proximate-ultimate distinction in terms of his own research, in his 1961 paper he used this dichotomy to argue for the uniquely *biological* value of the evolutionary approach to understanding the living world.[31]

George Gaylord Simpson was equally disgruntled with molecular biologists' apparent assumption that they held the key to the "secret of life," preferring instead to think of life as the "secret of DNA."[32] In 1961, the editors of *American Scientist*, the official magazine of the Sigma Xi Scientific Research Society, asked Simpson to write a "defense" of the biological study of organisms.[33] In his article, published the following year, he argued that at least two dimensions were necessary for any organizational scheme intended to classify biological studies. The first dimension was the level of biological organization. Here, Simpson drew a sharp line between the biology of whole organisms and research intended to reveal the cellular or subcellular processes of life. The second dimension was methodological, and he echoed Mayr's distinction between proximate and ultimate causes in biological investigations. Simpson distinguished between methodological reduction and composition, or the tendency to ask "how?" and "what for?" respectively.[34] Only answers to the latter question, he contended, were necessarily evolutionary and uniquely biological. When biologists merely asked how things work, what makes them go, how they function, he contended, "the investigator is not dealing with a lion, or any other organism at

30. Mayr, "Cause and Effect in Biology" (ref. 2), 1502; see also Ernst Mayr, "The Multiple Meanings of Teleological," in *Towards a New Philosophy of Biology: Observations of an Evolutionist* (Cambridge, MA: Harvard University Press, 1988), 38–66.

31. Beatty, "Proximate/Ultimate Distinction" (ref. 29).

32. George Gaylord Simpson, "The Crisis in Biology," *The American Scholar* 36 (1966–67): 363–77, on 374.

33. George Gaylord Simpson, "The Status of the Study of Organisms," *American Scientist* 50, no. 3 (1962): 36–45.

34. In 1962, Paul Weiss described a purely "reductionist" approach to developmental biology as untenable—how useless to put a chicken embryo in a blender and, after separating the resulting puree into its molecular components, ask: How do we get the chicken back? Paul Weiss, "From Cell to Molecule," in *Molecular Control of Cellular Activity*, ed. J. H. Allen (New York: McGraw-Hill, 1962), 1–72.

all, but with a chemical reaction in a test tube or some form of physical model." Such questions characterized the "mainly reductionist, lower-level subsciences of biology," like biophysics and biochemistry. Simpson contrasted such quasi-biologists with true biologists whose research had "no direct concern with the physical sciences," and instead relied on "exclusively biological" entities, like "whole organisms, populations, and communities."[35] For Simpson, current research in biochemistry, biophysics, neurophysiology, and genetics must eventually be related back to the level of the organism in order to sustain a coherent picture of biology as a whole. True biology was about organisms, from their interactions with each other and the ecological environment in which they lived, to the cellular machinery of which they were composed—molecular biology without reference to the organism was physical science in sheep's clothing.[36] Upon reading Simpson's article, Dobzhansky immediately wrote and congratulated him on a job well done. He also suggested that, "the proper counterpart to 'molecular biology' is 'organismic biology.'"[37]

Dobzhansky, for his part, voiced his increasing concerns over the effect of molecular biology a few years later in "Biology, Molecular and Organismic." In this paper, he suggested that it might seem appropriate to divide biology hierarchically according to nested levels of biological organization (as had Wright). However, Dobzhansky continued, this was impractical—far better was "a simple dichotomy of molecular and organismic biology, the latter name subsuming studies on all levels above a molecular one."[38] On the one hand, he commended Nagel's analysis for its insightful description of the divisions within modern biology. On the other hand, he (without naming names) dismissed as nonsensical the claims from molecular biologists who would either "declare a moratorium on organismic biology until such time when it can be reduced to molecular terms" or "argue that organismic biology is largely a finished business."[39] Dobzhansky associated such claims with the belief that all biological investigation should follow the lead of Descartes' "organism-the-machine" theory, contrasting this once again with organismic biology's reliance on Darwinian evolutionary explanations. Yet ideally these approaches should

35. Simpson, "Status of the Study" (ref. 33), 42–43.

36. Michael Dietrich, "Paradox and Persuasion: Negotiating the Place of Molecular Evolution within Evolutionary Biology," *Journal of the History of Biology* 31 (1998): 85–111.

37. Dobzhansky to Simpson, 13 Oct 1961, TDP, Series I: Correspondence, Folder GG Simpson.

38. Dobzhansky, "Biology, Molecular and Organismic" (ref. 2), 445.

39. Ibid., 448.

have been complementary, not agonistic. For Dobzhansky, the power of molecular biology to describe biological mechanisms shared by all living organisms resided in the common evolutionary history of all life, including humans.[40]

Could organismic biologists have advanced a more integrationist program? One possibility was Wright's assertion that all levels of biological organization (ecologic systems, interbreeding populations, multicellular organisms, cells, molecules) required different methodological approaches because new biological properties became manifest at each level. Yet such a scheme would grant molecular approaches a proper place in biology—an option Mayr in particular found anathema, while Simpson and Dobzhansky were more amenable. Another solution was to integrate across multiple levels of biological organization. Molecular biologists hoped that a solid understanding of DNA, proteins, and other biological molecules would eventually explain the order and diversity found at other levels of biological organization (the reductionist's dream). This option was obviously unappealing, as it would obviate a need for the very kind of biological research Mayr hoped to protect. Dobzhansky proposed a second form of integration: if evolutionary biologists accepted the gene as the level at which selection acted, then evolutionary theory would also be present at every level of biological organization identified in Wright's scheme.[41] Mayr rejected Dobzhansky's proposal as capitulating to the enemy. It might also have been possible to argue for a reverse-reductionist perspective—that a more thorough understanding of community-level interactions might eventually explain individual adaptations and the inner workings of cells and nuclei. Yet for Mayr this was not a viable strategy either, in part because of the diversity of organizational levels represented in organismic biology. No matter if the cellular and molecular biologists wouldn't stand for it; neither would the ecologists, physiologists, or population biologists.[42] So the strategy that Mayr hit upon, and Simpson largely supported, was his philosophical differentiation of proximate and

40. Hence his famous claim: "nothing makes sense in biology except in the light of evolution." Ibid., 449.

41. Smocovitis, *Unifying Biology* (ref. 15), 177; Dobzhansky, "Biology, Molecular and Organismic" (ref. 2), and Dobzhansky, "Are Naturalists Old-Fashioned?" (ref. 10).

42. Mark Borello, "Dogma, Heresy, and Conversion: Vero Copner Wynne-Edwards's Crusade and the Levels-of-Selection Debate," in *Mavericks, Rebels, and Heretics in Biology*, ed. Oren Harman and Michael R. Dietrich (New Haven: Yale University Press, 2008), 213–30. On the disunity of zoology in the early 1960s, see Kristin Johnson, "The Return of the Phoenix: The 1963 International Congress of Zoology and American Zoologists in the 20th Century," *Journal of the History of Biology* 42 (2009): 417–56. A similar strategy was adopted by British evolutionary theorists in the early 1960s, including Richard Dawkins, William Hamilton, George Price, and

ultimate causality in nature. Just as organismic biologists could not explain what was happening at a molecular level, neither could molecular biologists explain what was happening at an organismal level. In contrast to Wright's organizational scheme, evolutionary theory united all levels of biological organization except cells and molecules. The result, then, was two different and necessarily distinct forms of scientific inquiry (one biological and the other predominantly chemical or physical) that existed in a kind of mutual détente, each with its own philosophical grounding.[43]

In defending their turf, Simpson and Dobzhansky also picked up on a different aspect of Mayr's address to the annual Cold Spring Harbor Symposium on Quantitative Biology—that biologists' understanding of the future of humanity depended on organismal theories of evolution. For example, in Dobzhansky's letter to Simpson, he noted that he wished Simpson had emphasized that "organismic biology is fundamental for the understanding of man, while molecular biology is more important for the understanding of his ailments, and for finding a cure against colds."[44] Such a claim might have seemed unusual in the early 1960s, when human cytogenetics seemed to promise new insights into hereditary disease, the criminal mind, cancer research, and international population studies.[45] So when organismic biologists justified the importance

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John Maynard Smith. Their stance did not engender the same consternation witnessed in the U.S. during the same period.

43. For example, when molecular biologists began to address the "ultimate" questions so important to Mayr's description of biological research, they fell onto equally rough times: Jay D. Aronson, "'Molecules and Monkeys': George Gaylord Simpson and the Challenge of Molecular Evolution," *History and Philosophy of the Life Sciences* 24 (2002): 441–65; Marianne Sommer, "History in the Gene: Negotiations Between Molecular and Organismal Anthropology," *Journal of the History of Biology* 41, no. 3 (2008): 473–528; cf. Joel B. Hagen, "Naturalists, Molecular Biologists, and the Challenges of Molecular Evolution," *Journal of the History Biology* 32, no. 2 (1999): 321–41, and Joel B. Hagen, "George Gaylord Simpson, Morris Goodman, and Primate Systematics," in Cain and Ruse, eds., *Descended From Darwin* (ref. 15), 93–109.

44. Dobzhansky to Simpson, 13 Oct 1961, TDP, Series I: Correspondence, Folder GG Simpson. This was a swipe at Linus Pauling's molecular theory of disease; see Bruno Strasser, "World in One Dimension: Linus Pauling, Francis Crick and the Central Dogma of Molecular Biology," *History and Philosophy of the Life Sciences* 28 (2006): 491–512, and Bruno Strasser, "Linus Pauling's 'Molecular Diseases,' Between History and Memory," *Amercian Journal of Medical Genetics* 115 (2002): 83–93.

45. Soraya de Chadarevian, "'More Exciting than the Back of the Moon': Human Chromosome Images, 1950s–1960s," Meeting of the International Society for the History, Philosophy, and Social Studies of Biology, Brisbane, Jul 2009; Daniel Kevles, *In the Name of Eugenics: Genetics and the Uses of Human Heredity* (Cambridge, MA: Harvard University Press, 1995 [1985]), "Chromosomes—The Binder's Mistakes," 238–50.

of their approach to understanding people, they argued that only an organismic approach could help us understand human nature. Even though molecular biologists could identify the effects of large-scale mutations in people, understanding human social and sexual behavior required the attention of biologists who understood the processes of organic evolution under natural conditions.

By the 1960s, the tone and the target of evolutionists' theorizing about humanity was the essence of what it was to be human. For example, in 1958, psychologist Anne Roe and Simpson (Roe's husband) co-edited a volume on evolution and behavior. In the introduction, they contended that "the highest aim of evolutionary psychology is to provide a historical basis for and explanation of human psychology."[46] The volume was their attempt to incorporate animal behavior into the evolutionary synthesis and was based on a series of papers presented at a conference held a few years earlier. Similarly, in conjunction with the 1959 Darwinian Centennial Week at the University of Chicago, Mayr invited Julian Huxley, former Director General of UNESCO and student of animal behavior in his own right, to give a speech at the Museum of Comparative Zoology at Harvard. In his letter to Huxley confirming travel arrangements, Mayr explicitly described the purpose of Huxley's talk as an effort to buoy the importance of museums, and especially of systematics, to the future of biological research. Mayr feared that "molecular biology [was] increasingly taking over Biology departments," while more research on the "the whole animal and the whole plant" was still desperately needed. In Mayr's opinion, both university authorities and the broader public seemed oblivious to the importance of museums as useful research spaces outside of biology departments in which research on whole organisms could be protected. He added, "the study of man will get its greatest impetus from the type of people who center in natural history museums . . . one-sided support and emphasis on the type of biology that can be carried out in the experimental laboratories cannot achieve a harmonious growth of biology as a whole."[47] By 1964, when Mayr wrote to Konrad Lorenz, he had adopted "organismic" biology as shorthand for his position. "What is important . . . is to emphasize that in addition to that wonderful field of molecular biology, we have an equally wonderful field of organismic biology, a field which is becoming increasingly important for the understanding of man

46. Anne Roe and George Gaylord Simpson, eds., *Behavior and Evolution* (New Haven: Yale University Press, 1958), Introduction, 3.

47. All quotes in the paragraph are from the following letter: Mayr to Julian Huxley, 23 Oct 1959, EMP, HUGFP 14.15, Folder Julian Huxley.

and the planning of his future."[48] Mayr hoped that Huxley would choose to emphasize both of these points in his address at Harvard University.

Simpson, over the course of the 1960s, published a series of increasingly vociferous articles in which he began to insist upon the distinctive natures of the biological and physical sciences and to point to the unique ability of organismic biology to understand the nature of man.[49] In the early 1960s, he praised Mayr's paper on causality in biology as the clearest discussion he had read of the philosophical foundations of modern biological thought.[50] By later in the decade Simpson's tone became increasingly antagonistic. In a 1966 article entitled "The Biological Nature of Man," Simpson asserted that "nothing that has so far been learned about DNA has helped significantly to understand the nature of man or of any other whole organism."[51] In 1967, he resorted to calling the current obsession with molecular biology a combination of "monomania and schizophrenia" in the biological sciences. He deftly deflected the claim that molecular biology was modern biology by extending back the intellectual tradition on which it rested to at least the eighteenth century with the identification of the oxygen cycle in plants and animals, long before Darwin conceived of his theory of natural selection on which modern organismal biology was founded. Further, he suggested, "since biology is the study of life, and molecules, as such, are not alive, the term 'molecular biology' is self-contradictory."[52] He offered in its place "evolutionary organismal biology."[53] Simpson's discussions of molecular biology were never unilaterally negative,[54] but what I suggest by excerpting some of his pithier statements is, first, that during the 1960s tensions between organismic biologists and molecular biologists were increasing, and second, that it was during this time that Simpson, Dobzhansky, and Mayr came to identify themselves as organismic biologists.

48. Mayr to Konrad Lorenz, 20 May 1964, EMP, HUGFP 14.17, Folder Konrad Lorenz 1963–1964.

49. For a nuanced paper on how Simpson's role in the evolutionary synthesis and his attitude to molecular biology shaped his views on molecular evolution, see Aronson, "Molecules and Monkeys" (ref. 43).

50. George Gaylord Simpson, "Biology and the Nature of Science," *Science* 139, no. 3550 (1963): 81–88, on 83.

51. George Gaylord Simpson, "The Biological Nature of Man," *Science* 152, no. 3721 (1966): 472–78.

52. The last three claims all come from the same source: Simpson, "Crisis in Biology" (ref. 32), 367.

53. Ibid., 366.

54. Aronson, "Molecules and Monkeys" (ref. 43).

The synthesis architects also referred to themselves as "evolutionary biologists." In a way, evolutionary biology became a subset of organismic biology (which additionally included ecology, population biology, and animal behavior). Yet evolution simultaneously provided the theoretical justification for the organismal approach to nature envisioned by Mayr, Simpson, and Dobzhansky. Throughout the 1950s and '60s, organismic biologists strove to characterize their brand of biology as unique and irreducible to "molecularist" techniques or theories. They also increasingly framed their research in terms of its centrality to understanding the human condition as a way of claiming at least part of the mantle of modern biology for the organismic approach to scientific research.[55]

PROBLEM TWO, INSTITUTIONAL RECOGNITION

Organismic biologists, as they had come to call themselves, became wary of molecular biology in part because they believed molecular biologists were slowly gaining control of biology departments and scientific institutions across the United States, if not the world.[56] Edward O. Wilson's memoir, *Naturalist*, included a frank retelling of his memories of politics in the Biology Department at Harvard in the 1960s, including the dismissal of nonmolecular work as "classical" biology.[57] The so-called molecular biologists were in a bit of a tight spot, too. The huge promises of the discovery of the structure of DNA and the breaking of the genetic code were not followed immediately with hoped-for practical gains in medical research.[58] Molecular biologists claimed organismal

55. For the implications of this trend on behavioral research, see Erika Lorraine Milam, *Looking for a Few Good Males: Female Choice in Evolutionary Biology* (Baltimore: Johns Hopkins University Press, 2010), 135–59.

56. Ernst Mayr wrote to Theodosius Dobzhansky in 1972, remarking on his recent trip to the USSR. He noted that the USSR was quite similar to the United States in the relative funding and social position provided to so-called classical biology on the one hand, and physics, chemistry, and molecular biology on the other. Mayr to Dobzhansky, 19 Jun 1972, TDP, Series II: Correspondence with Ernst Mayr, Box 1.

57. Edward O. Wilson, "Molecular Wars," in *Naturalist* (Washington, DC: Shearwater Books, 1994): 218–37. Mayr considered Wilson's characterization of Watson unfair, and suggested by way of contrast that Watson "was not unfavorable to organismic biology"; as evidence, Mayr recounted several episodes where Watson had treated him with great respect and courtesy. Quoted in Haffer, *Ornithology, Evolution, and Philosophy* (ref. 4), 250.

58. Doogab Yi, "The Recombinant University: Technologies of Life and the Emergence of Biotechnology at Stanford, 1959–1980" (PhD dissertation, Princeton University, 2008).

research was old-fashioned, but they don't seem to have reacted defensively to the organismic biologists. The result: disputes over the nature of "modern" biology and the restructuring of biological institutions across the country, mainly at the instigation of organismic biologists.

In Wilson's account of the "Molecular Wars" at Harvard, he recalls that by 1960 concerned faculty within the Department of Biology had formed a caucus called the Committee on Macrobiology. Zoological faculty advocated abandoning their traditional systematic divisions in favor of a group united by their shared interest in higher levels of biological organization—organisms, populations, and ecosystems (rather than molecules or cells).[59] They hoped banding together would help protect their interests at the university level. Although the committee was a great success in the eyes of the participants, the name was not, and "Macrobiology" lasted only until the fall of 1962 when they found a more suitable name: the Committee on Evolutionary Biology. In reaction, other faculty in the department soon formed their own Committee on Cellular and Developmental Biology.[60] Wilson's prose adds some color. He described the attitude of the molecular biologists as inflammatory—"Let the stamp collectors return to their museums"—and the gut reaction of the evolutionary biologists as equally volatile—they "were not about to step aside for a group of test-tube jockeys who could not tell a red-eyed vireo from a mole cricket."[61]

Wilson noted that it was shortly after this informal split that biology departments across the country, including Harvard's, began to divide into departments of molecular, cell, and developmental biology, on the one hand, and

59. Wilson, *Naturalist* (ref. 57), 225.

60. According to the catalog listing of the Harvard University Archives, the second committee was in place by 1969, at least. At Berkeley, the Department of Molecular Biology formed separately from the Zoology Department; however, the general categorical distinctions were similar. The department defined two main goals within the biological sciences: taxonomy and "general" biology, the latter of which concerned "the universal attributes of life, just as physics is concerned with the universal attributes of matter." It was precisely this impression, that molecular biology and biochemistry should be categorized as "general biology," which the organismal biologists wished to dispel. "Report of the Committee to Plan the Scope and Activities of a New Department Concerned with Relating Biology and the Physical Sciences," 22 Oct 1962, Wendell M. Stanley Papers, Bancroft Library, University of California, Berkeley, BANC MSS 78/18c, Box 23, Folder History of M.B. Department, pp. 1–2. Quoted in Angela Creager, "Wendell Stanley's Dream of a Free-Standing Biochemistry Department at the University of California, Berkeley," *Journal of the History of Biology* 29, no. 3 (1996): 331–60, on 355–56.

61. Wilson, *Naturalist* (ref. 57), 227–28.

departments of evolutionary or population biology, on the other.[62] This coincided with a push to unify botany and zoology departments—a trend that largely pleased zoologists, but left botanists feeling far more ambivalent.[63] When the University of California, Irvine, opened its doors in 1965, in place was a Department of Organismic Biology. The State University of New York, Stony Brook, created a Department of Ecology and Evolution in 1969. Around the same time, the Department of Systematics and Ecology was formed at the University of Kansas, as was the Committee on Evolutionary Biology at the University of Chicago. Similarly, the Zoology Department at University of California, Davis, formed two "area committees" in the early 1970s—Organismal and Environmental Biology, and Cell and Molecular Biology.[64]

Wilson also intimated that the "molecularists" at Harvard were willing to let the future of the department rest on official recognition outside the university, such as Nobel Prizes (for which he notes evolutionary biologists were ineligible) and the number of publications in *Nature*, *Science*, and the *Proceedings of the National Academy of Sciences*.[65] To this list I also add the National Medal of Science (awarded by the President of the United States through the National Science Foundation, and for which evolutionary biologists were eligible) and election to the National Academy of Sciences.

The National Medal of Science (NMS) was established by Congress in 1959, following the Soviet launch of the Sputnik satellite, and was awarded for the first time in 1962 to engineer Theodore von Kármán, the "dynamic aerodynamicist."[66] In subsequent years, scientists were recognized for four categories of research: physical sciences, biological sciences, mathematics, and engineering. Within the category of the biological sciences, organismic biologists proved quite successful. President Johnson awarded Theodosius Dobzhansky an NMS because of his role as "a world leader in experimental population

62. Ibid., 226. Harvard University's Department of Organismic and Evolutionary Biology, however, was not created until the early 1980s.

63. Appel, *Shaping Biology* (ref. 6), 224. Appel suggests that a number of botanists felt they should instead join forces with cellular and molecular biologists rather than playing second fiddle to zoologists.

64. The "area committees" at Davis separated into two departments in 1993. These dates are reconstructed by following key biologists' departmental affiliations as listed on their publications currently archived in JSTOR.

65. Wilson, *Naturalist* (ref. 57), 229.

66. Special to the *New York Times*, "Dynamic Aerodynamicist: Theodore von Karman," *New York Times,* 19 Feb 1963; Robert C. Toth, "Von Karman Gets U.S. Science Prize," *New York Times,* 19 Feb 1963.

genetics and its application to the problem of evolution."[67] Dobzhansky was one of two biologists to be awarded the medal in 1964; the other was Marshall Nirenberg for his work on the genetic code.[68] When George Gaylord Simpson was awarded an NMS the following year, the official citation described Simpson as "a pioneer in synthesizing the findings of genetics and paleontology and applying them to the study of evolution."[69] Ernst Mayr was similarly honored in 1969, and Wilson in 1976. All told, between 1962 and 1980, organismic biologists received almost twenty percent of the medals awarded for research in the biological sciences.[70] However, no financial remuneration accompanied this award because a 1962 bill to include up to $10,000 along with the NMS failed to pass the House of Representatives. Opponents of the bill suggested that money would "cheapen" the medal and that a nonmonetary award was in keeping with national tradition (no cash awards are given with medals for military bravery, for example).[71]

Money for organismic research was certainly available through the National Science Foundation (NSF). In 1954, for example, over sixty percent of all federal funding for systematics was disbursed through the NSF. Molecular and regulatory biologists, by way of contrast, received less than five percent of their total federal funding through the NSF.[72] Even a decade later, systematics and ecology received about twenty percent of NSF's monies, although NSF was supplying only five percent of federal funding for biological research by 1963 (the growth of the National Institutes of Health played a large role in the expansion of federal funds for primarily molecular, cellular, and neurobiological

67. Burton Lindheim, "Theodosius Dobzhansky, Geneticist, Is Dead at 75," *New York Times,* 19 Dec 1975.

68. Special to the *New York Times*, "Medal of Science Is Awarded to 11," *New York Times,* 28 Nov 1964.

69. John D. Pomfret, "Johnson Names 11 for Science Medals," *New York Times,* 12 Dec 1965.

70. About an equal number were awarded for agricultural advances, and about thirty percent each to medical and molecular research. See the full list of recipients at www.nsf.gov/od/nms/results.cfm?action=find (last accessed on 13 May 2010).

71. "Science Cash Award Opposed," *New York Times*, 7 Aug 1962; "House Rejects Plan on House Awards," *New York Times*, 9 Aug 1962. By way of contrast, the Darwin Medal, awarded biannually by the Royal Society of London for work pertaining to Darwin's research, was awarded to Ronald Fisher (1948) and J. B. S. Haldane (1952) before either Julian Huxley (1956) or Simpson (1962) received the honor. Sewall Wright (1980) also received the medal before Ernst Mayr (1984). Even this award, however, came with only £1000. For a list of award recipients, see http://royalsociety.org/Darwin-Medal/ (last accessed on 13 May 2010).

72. Appel, *Shaping Biology* (ref. 6), 150–51.

research).[73] In other words, systematic and environmental research continued to receive a large proportion of NSF funding through the 1970s, even as federal funding across the board for cellular and molecular research quickly outpaced organismic funds. It seems likely that systematic research fared so well at the NSF throughout these difficult decades because systematicists could control their own budget. When the Division was reorganized in 1964, the four sections thus created still provided insulation for systematic research—cellular biology, environmental and systematic biology, molecular biology, and physiological processes.[74] The success of the organizational structure at NSF may have provided a model for organismic biologists, like Mayr, who sought institutional protection in other forums.

The National Academy of Sciences (NAS) proved a much stickier wicket for organismic biologists. Wilson was elected in 1969 in the midst of a continuing struggle among biologists over the internal organization of Class II of the NAS: the Biological and Behavioral Sciences. (The other designations were Class I: Physical and Mathematical Sciences, and Class III: Engineering and Applied Sciences.) Class II consisted of nine sections: botany, zoology (previously called zoology and anatomy), physiology, microbiology (previously called pathology and microbiology), anthropology, psychology, biochemistry, and two brand new sections, medical sciences and genetics.[75] Members were nominated by section—an informal candidate needed to garner at least two-thirds of the votes of a single section or one-half of the votes of any two sections within a class to be nominated—but were elected within a particular Class, and approved by the entire membership of the NAS.[76] Once elected, members could chose to

73. NSF funded $63.85 million on ecological and systematic research between 1967 and 1973, out of a total of $321.42 million for all biological research during the same years, excluding grants to special facilities and biological oceanography which fell outside the purview of the Division of Biological and Medical Sciences; Appel, *Shaping Biology* (ref. 6), 240. In 1963, NSF spent $41.65 million on research in the life sciences, a small proportion of the $891.91 million in federal funds devoted to research in the life sciences that same year (in addition to NSF, Appel collates funds from the U.S. Department of Agriculture, Army, Navy, Air Force, NIH, Department of Health, Education, and Welfare, Department of the Interior, the Atomic Energy Commission, and the National Aeronautics and Space Administration); ibid., 146. An analysis of organismal biologists efforts to lobby the NSF is well worth investigating, but beyond the bounds of this paper.

74. Ibid., 280–84.

75. *Annual Report—National Academy of Sciences, National Academy of Engineering, Institute of Medicine, Fiscal Years 1969 to 1970* (Washington, DC: National Research Council, 1975), 185.

76. Ibid., 174–81. These pages describe the rules and procedures for nomination and election at that time. Each section sent the names of its nominees to the class membership committee, which ranked the nominees in order of preference and created a combined list (a preference ballot)

which section they wished to belong, regardless of which section had been responsible for their nomination. The first major barrier to being elected, then, resided in the section-controlled process of nomination. This provided part of the motivation for Dobzhansky choosing to remain in the zoology section even after the new section for genetics was created—he feared that genetics would end up including people of such diverse interests that it would inevitably become either "unwieldy" or "dominated by a small clique."[77]

Mayr was slowly but surely gathering support from his closest friends to reorganize Class II in a way that he felt more accurately reflected the current divisions within the biological sciences. He had written to Simpson seeking support for revising the current electoral system. Simpson replied that something needed to be done in light of the low representation of paleontologists in the NAS, especially in comparison to geophysics: "Geophysics has 39 Academy members, and all other geological sciences put together have 42, representing specialties incomparably more diverse and professionals many times more numerous than in geophysics."[78] Mayr responded in turn by pointing to the connection between the woes of organismic biologists in Class II and Simpson's troubles in Class I.

> One of the major troubles has been the fact that the physical scientists had captured the Council of the Academy and prevented all changes. Prior to last July 1 all officers of the academy were physical scientists. They invariably had a

that it sent on to the home secretary. Each Class could advance only a certain number of nominees per year as determined by the Council, and the preference ballot created at this stage could contain up to one hundred fifty percent of the stated quota. The home secretary sent to the entire Class membership the class preference list, a statement of accomplishment for each scientist on the list, and the voting record from each section and the nominating group. Each member was asked to vote for at least a third and no more than one half of the names on each Class list. The home secretary then prepared two lists, one containing the names of the nominees ordered by the number of votes they had received up to the quota allowed for each section, and a second containing the names of the remaining candidates, also ranked by number of votes. These lists were distributed to the membership of the NAS present at the annual meeting, where any nominee's name (and their placement on either the first or second list) could be revisited. The names on the first list were then declared elected by a two-thirds vote of members present at the annual meeting.

77. Dobzhansky to Clifford Grobstein, Office of the Vice Chancellor, 23 Aug 1973, TDP, Series I: Correspondence, Folder NAS #4. In fact, many of the *Drosophila* population geneticists chose to remain in zoology, including Richard Lewontin, I. Michael Lerner, John Moore, and Bruce Wallace. On the other hand, Curt Stern, James Crow, and Sewall Wright moved into the newly created genetics section (which contained 32 members its first year). See the *Annual Report—1969 to 1970* (ref. 75), 232–36.

78. Simpson to Ernst Mayr, 20 Nov 1969, EMP, HUGFP 74.7, Box 18, Folder 1063.

> majority of approximately 11 to 5 on the Council. When the structure of classes was introduced I fought a vigorous but losing battle against having the biochemists (more than half of whom had their actual laboratories in chemistry departments) added to Class II.[79]

If Mayr's letters had little effect on Simpson, there was sufficient concern within Class II so that by 1973, negotiations for a reorganization of the sections were already underway.[80] Dobzhansky wrote to the Office of the Vice Chancellor adding his vote of support for some kind of change: "The present section structure was logical one half a century ago," he suggested, "but a reform is long overdue."[81] Under discussion was a proposal to replace the previous sections with new ones: biochemistry, molecular biology and biophysics, cellular and developmental biology (including microbiology), organismal biology, integrative and behavioral biology, and ecology and population biology.[82] Applied biology and medicine had already been granted their own class and so were beyond the purview of the negotiations. Several concerns remained. Should the existing section of genetics be kept, or eliminated and its members redistributed according to their preference in the new sections? Should molecular biology and biophysics really be lumped together in the same section? Should that section be additionally combined with biochemistry to form a section called subcellular biology or molecular genetics? What to do with the physiologists, especially the plant physiologists? Should developmental biology be called out in the title of a section?

Negotiations continued through 1975, and Mayr wrote repeatedly to Philip Handler, President of the National Academy of Sciences, unhappy with the persisting imbalances in the NAS elections.[83] "One lesson is rather clear to me," Mayr insisted, "which is that a section consisting of a mixture of cellular and organismic biologists is a very unnatural body. The two camps know nothing about each other." Although some of the good organismic candidates could in

79. Mayr to George Gaylord Simpson, 12 Dec 1969, EMP, HUGFP 74.7, Box 18, Folder 1063.

80. See TDP, Series I: Correspondence, Folder NAS #4.

81. Theodosius Dobzhansky to Cifford Grobstein, 23 Aug 1973, TDP, Series I: Correspondence, Folder NAS #4.

82. Memorandum, Class II Members, 26 Jul 1973, TDP, Series I: Correspondence, Folder NAS #4. On the relationship between biophysics and molecular biology, see Nicolas Rasmussen, "The Mid-Century Biophysics Bubble: Hiroshima and the Biological Revolution in America, revisited," *History of Science* 35, no. 109 (1997): 245–94, and de Chadarevian, *Designs for Life* (ref. 5).

83. Mayr to Handler, 1 May 1975, 3 Jul 1975, EMP, HUGFP 74.7, Box 23, Folder 1229.

theory be supported by the Section of Genetics (population geneticists), he added, "in recent years that section has supported only molecular geneticists. Too bad, but a fact."[84] Handler responded by confirming that yes, indeed, plans were still underway to reorganize the sections within Class II to mitigate such problems. He noted that a questionnaire was being sent to all members of Class II asking for an evaluation of the new proposal. In this proposal, Handler promised, was a section "called something like 'Population Biology, Evolution, and Ecology.' While this may not be an ideal combination to deal with the problems you describe, such a section would indeed permit opportunity for competition among such individuals . . . quite independent of any competition among the 'molecular biologists.'"[85]

A letter from Theodore H. Bullock, chair of the NAS Zoology Section, to other members of section described the new proposal in more detail.[86] In 1974, those members present at the official meeting of Class II had voted to rearrange the sections as follows: biochemistry, cellular and developmental biology, physiological biology, neurobiology, population biology and ecology, genetics, and botany. Additionally, the letter specified, that at the 1975 official meeting of Class II, members decided that the matter needed to be settled by a mail ballot of the entire membership. It had taken three years to hammer out this compromise, and all involved hoped the ballot would be approved. In answer to the questions raised in 1973, genetics was kept as a separate section, as was biochemistry. The proposed section of molecular biology and biophysics was scrapped entirely, and a new section created to accommodate the physiologists left out of the original proposal. The new proposal passed, with the only amendment the addition of the word "evolution" to the fifth section, making it "population biology, evolution, and ecology," as Handler had promised.[87]

It is hard to calculate what effect this reorganization had on the ability of organismic biologists to elect members in their field to the NAS. What is clear is that before the reorganization, Mayr and Dobzhansky advanced the names

84. Mayr to Handler, 1 May 1975, EMP, HUGFP 74.7, Box 23, Folder 1229. Mayr's problems with microbiologists are well known. See, for example, Carl R. Woese, "Default Taxonomy: Ernst Mayr's View of the Microbial World," *Proceedings of the National Academy of Sciences* 95 (1998): 11043–46.

85. Handler to Mayr, 19 May 1975, EMP, HUGFP 74.7, Box 23, Folder 1229.

86. Bullock to Members of the Zoology Section, National Academy of Sciences, 2 May 1975, TDP, Series I: Correspondence, Folder NAS #4.

87. *Annual Report—National Academy of Sciences, National Academy of Engineering, Institute of Medicine, Fiscal Years 1975 and 1976* (94th Congress, 2nd Sess., Senate Document No. 94–258: National Research Council, 1975), 188.

of three scientists whom they thought ought to be elected. They made sure not to put all the names forward at once to avoid splitting the vote of organismic biologists; they strategized about which section in which to advance their names; and they wrote letters to their colleagues casually mentioning the outstanding achievements of their nominees. Yet despite their efforts, these nominees repeatedly failed to obtain a sufficient number of votes. After the reorganization, however, all three were successfully elected: Hampton Carson in 1978, Francisco Ayala in 1980, and Robert Selander in 1982.[88]

It was also during this time that Richard Lewontin and Bruce Wallace, less than three years after their election, submitted letters of resignation to the NAS over the classification of research conducted by NAS members for the Department of Defense and other branches of the federal government during the Vietnam War. In a recent interview, Lewontin recounted his decision. Certainly, he agreed that he was conscious of his role as a social critic and wanted to send a clear message to the academy: either all such work stop immediately, or he would resign! Well, the work didn't stop and he was as good as his word. When time came to vote on his resignation, the members of the Academy accepted his resignation with regret.[89] The maneuvering of the members of the NAS was another reason Lewontin cited for his resignation: "I realized around that time that the existence of a thing called the National Academy of Sciences, an honorary organization to which every scientist wants to aspire, is destructive of intellectual life. The whole notion of the chief motivating element being prizes, honorary degrees, personal prestige, memberships in academies, that really turned me off."[90] As far as I can reconstruct, after Lewontin's resignation, Thomas Eisner and Bruce Wallace proposed a new bylaw that would declassify all research conducted by members of the NAS. When this proposal did not pass, Wallace also submitted a letter of resignation. Wallace's resignation was not approved by the membership, however, in hopes that he would reconsider, which he did. Both Mayr and Dobzhansky were livid at Wallace for his letter

88. Dobzhansky to Mayr, 5 Jun 1973; Dobzhansky to Mayr, 22 Jul 1973; Dobzhansky to Mayr, 4 Dec 1974; Mayr to Dobzhansky, 12 Dec 1974; Dobzhansky to Mayr, 8 Oct 1975, TDP, Series II: Correspondence with Ernst Mayr, Box 1.

89. *Annual Report—National Academy of Sciences, National Academy of Engineering, Institute of Medicine, Fiscal Years 1973 and 1974* (94th Congress, 1st Session, Senate Document No. 94–41: National Research Council, 1975), 143.

90. "Science and Politics: Conversation with Richard C. Lewontin," Conversations with History, Institute of International Studies, University of California, Berkeley, p. 5, "Scientist as Activist," http://globetrotter.berkeley.edu/people3/Lewontin/lewontin-con0.html (last accessed on 13 May 2010).

of resignation, perhaps in small part because they consistently lamented the lack of organismic biologists in the Academy.[91] What is clear from this episode is that although Mayr saw his chief enemy as molecular biology, others had different agendas—in this case, the fight against the military-industrial complex—and these agendas did not always accord.

After the new sections were created, Mayr's interest in maintaining the boundary between organismic and molecular biology continued apace. In 1983, he wrote to a fellow NAS member describing what he saw as the "real meaning" of their section, namely systematics, evolution, and population biology. In the years since 1975, Mayr complained, he had come to regret the addition of ecology because of its breadth of field. Several of the nominees put forward by ecologists in the section for possible election worked on the "chemical and physical aspects of the environment." Their proper place at the NAS, he intimated, was in someone else's section, like applied biology. As "population biology, evolution, and ecology" was able to elect a maximum of two people each year, Mayr choked at the idea of giving up even one of these places to an ecologist with affinities for the physical sciences.[92]

The political negotiations Lewontin found so distasteful were also extremely effective. Both at their home universities and at institutions such as the NSF and the NAS, organismic biologists succeeded in carving out an enduring and separate space for themselves in the landscape of the American biological sciences.

PROBLEM THREE, HISTORY OF BIOLOGY

The efforts of organismic biologists to codify their collective identity through the history of evolutionary theory echoed their concerns over their identity as philosophically distinct from molecular biology, and their status in biology departments and at the National Academy of Sciences. Over the course of the 1960s, Mayr became increasingly fascinated with the history of biology and by the 1970s was working simultaneously on two major historical projects designed to place organismic biology in its proper historical context: his 1974 conferences on the evolutionary synthesis that culminated several years later in the publication of *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, and his history of biology, *The Growth of Biological Thought: Diversity,*

91. Dobzhansky to Mayr, 22 Jul 1973, TDP, Series II: Correspondence with Ernst Mayr, Box 1.
92. Mayr to Francisco Ayala, 24 Aug 1983, EMP, HUGFP 74.7, Box 30, Folder 1361.

Evolution, and Inheritance.[93] He intended each as a philosophical defense of what he considered true, nonreductionist biology.

The historical narratives Mayr produced in the 1970s and '80s served as far more than mere records of intellectual heritage. In 1972, Mayr wrote to ethologist Niko Tinbergen, exclaiming, "it is rather remarkable how long biology was dominated by the misconception that one should ask the same questions in biology as in physics or chemistry. I have been fighting this for as long as I can remember . . . If I am lucky I will be able to express this in my historical studies."[94] By giving organismic biology its own historical legacy, Mayr supplied another dimension to its identity.

His commitment to advancing the prestige of organismic biology by calling attention to the contributions of systematics and paleontology to the synthesis was repeated time and again in his correspondence surrounding the 1974 conferences on the *Evolutionary Synthesis*. For example, in a letter to George Gaylord Simpson, Mayr wrote, "as far as the conference on the 'Synthesis' is concerned—confidentially—I want to counteract the present historiography which gives just about all the credit to the geneticists. They shall have all the credit they deserve, but not more."[95]

In his correspondence with historian of science Mark Adams about the conference, Mayr repeated this point again. He noted that Adams' essay rightly emphasized the attitudes of the leading Darwinians in the early twentieth century, "that Mendelism was the enemy of Darwinism." Therefore, "the contribution of genetics to the synthesis has been greatly exaggerated."[96] Because Mayr believed so strongly that the existing histories of biology were biased in favor of mechanistic biology, he felt no compunction about producing what he suspected were histories biased in favor of organismic biology. If he were wrong, Mayr contended, his scientific contemporaries and later historians would untangle the politics from the truth.

93. On the origins of Mayr's interest in the history of evolutionary theory as connected to the Darwinian centennial celebrations of 1959, see Smocovitis, "1959 Darwin Centennial Celebration" (ref. 3); Smocovitis, "Unifying Biology" (ref. 11), 59–63; Thomas Junker, "Factors Shaping Ernst Mayr's Concepts in the History of Biology," *Journal of the History of Biology* 29, no. 1 (1996): 29–77; Mayr and Provine, eds., *Evolutionary Synthesis* (ref. 24); Ernst Mayr, *The Growth of Biological Thought: Diversity, Evolution, and Inheritance* (Cambridge, MA: Belknap Press, 1982).

94. Mayr to Tinbergen, 14 Apr 1972, EMP, HUGFP 14.17, Folder Nikolaas Tinbergen, 1970–1974.

95. Mayr to Simpson, 27 Aug 1973, GSP, Series I: Correspondence, Folder Ernst Mayr #3.

96. Mayr to Mark Adams, 29 Sep 1978, CES, Box 1, Folder Mark Adams.

With his letter, Mayr included a questionnaire for Simpson to complete. Mayr sent the same questionnaire to all biologists he felt would be key to revising the history and he also sent copies to many of the historians attending the conference (not to fill out, but for reference).[97] The questionnaire itself consisted of four parts. Personal information came first, and included questions about professional associates, teachers, opponents, and publications. The second part of the questionnaire asked respondents to rank various factors in terms of their relative influence on delaying the synthesis (which took place, Mayr noted, seventy-five years after Darwin published *On the Origin of Species*). The third part contained questions that sought to establish both arguments used by opponents of Darwinian evolution and positive contributions to the synthesis. The final section requested information about professional contacts with biologists outside respondents' primary field of expertise, and respondents' views during the synthesis period on mutation, variation, the environment, natural selection, the nature of evolution, recombination, gene and genotype, fitness, species concept, and speciation. The entire questionnaire was geared toward reconstructing a list of the theoretical misconceptions that had prevented biologists from achieving a synthesis earlier, and a list of positive factors (people and theories) responsible for overcoming these past misconceptions.

Simpson was irritated by the questions, as he felt they set the playing field before anyone had a chance to object. He wrote to Mayr, "I think that your conclusions are distorted not by commission but by omission."[98] Mayr responded almost immediately.

> I knew that and I emphasized my bias. It is precisely such a conference which will bring out such omissions . . . I have always felt that nothing clears the air as

97. Mayr sent the questionnaire out in several batches to at least the following people—19 Feb 1974: G. G. Simpson, Mark Adams, Garland Allen, Richard Burkhardt, Frederick Churchill, William Coleman, Michael Ghiselin, Camille Limoges, and William Provine; 21 Feb 1974: R. C. Lewontin; Feb 25, 1974: G. L. Stebbins, Th. Dobzhansky, and E. B. Ford; 27 Feb 1974: I. B. Cohen, G. Holton, and A. H. Durpree; 1 Mar 1974: B. Rensch, and M. Lerner; 5 Mar 1974: E. Bosiger; 6 Mar 1974: L. C. Dunn, H. Carson, and C. Stern; 24 Apr 1974: B. Glass; 13 Jun 1974: E. Olsen; 14 Jun 1974: N. V. Timofeeff-Ressovsky.

98. Simpson to Mayr, 8 Sep 1973, GSP, Series I: Correspondence, Folder Ernst Mayr #3. Simpson sent a copy of his answers to the questionnaire not only to Mayr, but to a number of his other friends as well. Additional copies survive: Simpson to Dobzhansky, 18 Mar 1974, TDP, Series I: Correspondence, Folder GG Simpson; "Answers to Questionnaire Concerning the Evolutionary Synthesis," CDP, C.104, H.165.

> much as a clear, even if blunt, statement of opinions. If they are wrong they will surely be refuted almost immediately. This is the beauty of a conference, that an unfounded claim can be refuted at once.[99]

Let us consider, for a moment, why Simpson found Mayr's questionnaire so aggravating: it was Mayr's contention that the evolutionary synthesis had been *delayed* by geneticists and in many ways represented a return to classical Darwinism. Simpson wrote with his usual flair, calling Mayr's historical characterization an "oversimplification to the point of falsification." Simpson continued, "there was no 'return' but a continuous development from 1859 to now, for Darwinism, Neo-Darwinism and synthetic theories formed an intellectual sequence that always had adherents and that continuously progressed even when it had more opponents than it does now."[100] Certainly, Simpson lamented the current state of affairs in which neither the average molecular biologist nor the average organismic biologist understood the other's research. During the synthetic period, by comparison, he suggested that communication between disparate biological fields was far more common. Because the "best minds" had been interested in evolutionary questions, "the synthesis . . . developed normally or even rather rapidly as the history of science goes." By the time Simpson was well into the heart of the questionnaire, he interspersed his answers with grating criticisms—"this question is also poorly phrased"—but he answered every question in great detail.

Simpson was not the only critic of Mayr's questionnaire. At issue for many of his respondents was Mayr's assertion there had been an almost total neglect of ultimate causes and interest in evolutionary theory between Darwin and the 1930s. Respondents on both sides of the Atlantic pointed to the important contributions of mathematical geneticists in changing their thoughts about evolution during the 1920s. British ecological geneticist E. B. "Henry" Ford suggested that it was mathematician and theoretical population geneticist Ronald Fisher's 1927 paper, "On Some Objections to Mimicry Theory—Statistical and Genetic," that constituted the "true start of the modern synthesis."[101] His answers to the questionnaire made it clear that Fisher had

99. Mayr to Simpson, 17 Sep 1973, GSP, Series I: Correspondence, Folder Ernst Mayr #3; Ernst Mayr, "Recent Historiography of Genetics," *Journal of the History of Biology* 6 (1973): 125–54, and *Growth of Biological Thought* (ref. 93), 9.

100. Simpson to Mayr, 8 Sep 1973, GSP (ref. 98).

101. R. A. Fisher, "On Some Objections to Mimicry Theory—Statistical and Genetic," *Transactions of the Royal Entomological Society of London* 75 (1927): 269–78. "Questionnaire Concerning

been a personal and intellectual source of inspiration for him.[102] Julian Huxley was also very committed to the importance of genetics as a discipline sparking interest in evolutionary theory.[103] Among the American respondents, *Drosophila* and human geneticist Curt Stern identified both J.B.S. Haldane and Sewall Wright as important contributors to his intellectual development (as well as Charles Darwin, August Weismann, and Dobzhansky), and fondly remembered his conversations with Alfred Sturtevant about evolutionary theory during the two years he spent working in Thomas Hunt Morgan's laboratory studying fruit flies in the 1920s.[104] Even Simpson suggested that when he was working out his own synthesis, he read and used works by Fisher and Haldane. He noted that he was "a bit late in getting to Sewall Wright, but did so in time," and had cited seven of Wright's papers in *Tempo and Mode in Evolution*.[105] Developmental embryologist Viktor Hamburger succinctly responded—"there was no 'almost total neglect of ultimate causes'" before the 1930s.[106]

Another issue for many of the respondents came from the secondary questions inquiring as to why the synthetic theory had not been adopted by botanists for so long, or by developmental biologists at all. Unsurprisingly, scientists who worked in these fields took exception to Mayr's characterization of their intellectual heritage. Hamburger insisted that the synthesis was not "missing" in developmental biology, and referred Mayr to his own work in Germany, that of Ivan Ivanovich Schmalhausen in the USSR, and of Conrad Hal Waddington in England.[107] However, he continued, their collective integration of evolutionary

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the Evolutionary Synthesis, Answers by E. B. Ford," page 5, TDP, Series I: Correspondence, Folder E.B. Ford #2.

102. Follow-up questions and answers to Ford's original questionnaire can be found in Edmund Brisco Ford Papers, Special Collections and Western Manuscripts, Bodleian Library, University of Oxford, Oxford, UK, National Cataloguing Unit for the Archives of Contemporary Scientists, 14.7.89, C.2646, A.9.

103. Already in poor health when he received the questionnaire, Julian Huxley was unable to attend the meeting, and Juliette Huxley (his wife) helped him complete the questionnaire. "Julian Huxley," CES, Box 1, Folder Julian Huxley.

104. "Curt Stern," CES, Box 2, Folder Curt Stern. On life in the Morgan lab, see Robert Kohler, *Lords of the Fly: Drosophila Genetics and the Experimental Life* (Chicago: University of Chicago Press, 1994).

105. Simpson to Mayr, 8 Sep 1973, GSP (ref. 98). For more on Wright's influence on the synthesis architects, especially Simpson and Dobzhansky, see Provine, *Sewall Wright and Evolutionary Biology* (ref. 24).

106. Viktor Hamburger to Ernst Mayr, 27 Oct 1975, CES, Box 1, Folder Viktor Hamburger.

107. Notably absent here is any mention of Richard Goldschmidt's work in the United States. See Dietrich, "Richard Goldschmidt's 'Heresies'" (ref. 9), for an account of how Goldschmidt became persona non grata to the synthesis architects. For a picture of Hamburger's role in the

and developmental research had never made it into the canon of the "Modern Synthesis"—a failure he laid at the feet of Mayr, not the developmental biologists. Along similar lines, botanist and synthesis architect G. Ledyard Stebbins denied Mayr's implication that plant evolutionists did not contribute actively to the synthesis.[108] They had, Stebbins asserted, "but the zoologists who formulated the theory ignored or minimized their contributions, because they didn't conform well to theories based on observations with animals." A particularly thorny issue for Stebbins was Mayr's insistence on the primacy of geographic isolation as the basis of speciation. He wrote, "I can't help being offensive. If on this basis you don't want me in Boston, that's OK with me. What is normal for birds, may not be normal for plants."[109]

It is not my concern here whether Mayr got his history (or his biology) right. Some of his chosen respondents agreed with all of his interpretations. French population geneticist Ernst Bösiger, for example, wrote that the synthetic theory as he understood it was "in reality quite different from the theoretical and mathematical models" of Fisher, Haldane, and Wright.[110] Instead, the point is that despite their disagreements over the historical and biological content of the meeting, they all wanted to participate.[111] It was an exciting and important step in writing the history of a field they wanted to remember and protect. As such, they agreed with Mayr's original premise—they too wanted to correct a bias in the existing literature on the synthetic period, even if they disagreed over the details and the nature of that bias.[112] The end result was a history of evolutionary

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evolutionary synthesis, see Gregory Davis, Michael Dietrich, and David Jacobs, "Homeotic Mutants and the Assimilation of Developmental Genetics into the Evolutionary Synthesis, 1915–1952," in Cain and Ruse, eds., *Descended from Darwin* (ref. 15), 133–54.

108. Vassiliki Betty Smocovitis, "Keeping Up with Dobzhansky: G. Ledyard Stebbins, Plant Evolution, and the Evolutionary Synthesis," *History and Philosophy of the Life Sciences* 28 (2006): 11–50; Anthony D. Bradshaw and Vassiliki B. Smocovitis, "George Ledyard Stebbins," *Biographical Memoirs of Fellows of the Royal Society* 51 (2005): 398–408.

109. These quotes come from a letter Stebbins wrote to Mayr the day after receiving the questionnaire. Stebbins to Mayr, 3 Mar 1974, CES, Box 2, Folder G. Ledyard Stebbins. For Stebbins' answers to the questionnaire itself, see CDP, C.104, H.166.

110. Ernst Boesiger, "Answers to the Questionnaire Concerning the Evolutionary Synthesis," CDP, C.104, H.165.

111. Even Simpson, who always preferred writing things down to talking with people, sought to preserve his answers for posterity by distributing them to multiple sources. See Wilson's description of Simpson in *Naturalist* (ref. 57), as well the articles by Aronson, "Molecules and Monkeys" (ref. 43), and Joe Cain, "A Matter of Perspective: Multiple Readings of George Gaylord Simpson's *Tempo and Mode in Evolution*," *Archives of Natural History* 30, no. 1 (2003): 28–39.

112. Darlington's papers additionally include copies of the questionnaires submitted by Hampton Carson (CDP, C.104, H.166), Bernard Rensch (CDP, C.104, H.165), and Dobzhansky (CDP,

theory in the twentieth century designed to unite organismic biologists with a common set of historical questions (if not answers).

Although Mayr maintained that voices of opposition would mitigate any of his claims that were overly biased, in practice he prevented those voices from being heard. For this reason, co-editing the *Evolutionary Synthesis* volume with William Provine was more of a challenge than Mayr anticipated, given Provine's affection for Sewall Wright, population genetics, and precisely the kind of history Mayr was trying to dispel. Provine's first attempt to write an epilogue for the *Evolutionary Synthesis* was a point-by-point refutation of Mayr's introduction (which had served as the keynote to the conferences). After reading the draft, an enraged Mayr wrote to Provine: "The reason I slanted the keynote was that the literature on the split in evolutionary biology between 1900 and 1935 up to now was totally one-sided, all written by geneticists."[113] To pacify Mayr, Provine rewrote the epilogue completely, omitting all references to Mayr's keynote.[114] Mayr carefully managed the content and conclusions of the *Evolutionary Synthesis* to emphasize the importance of the newly constructed vision of organismic biology during the synthesis period.[115]

Mayr never intended his other historical project, *The Growth of Biological Thought*, to be the history of *all* biological research either. Rather, he planned the book as the first of a two-volume set on the history of biology: *The Growth of Biological Thought* would cover the study of ultimate causes in biology, and

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C.104, H.166). Dobzhansky's follow-up questions and answers can be found in his own papers, TDP, Series I: Correspondence, Folder Ernst Mayr #6. Boris L'vovich Astaurov's answers to the questionnaire are also at the Americal Philosophical Society, CES, Box 1, Folder Astaurov, BL.

113. Mayr to Provine, 3 Jan 1978, CES, Box 1, Folder William Provine #2.

114. Provine to Mayr, 6 Feb 1978, CES, Box 1, Folder William Provine #3. Mayr suggested in his letter that Provine should publish a separate paper (not in the conference volume) in which he was free to argue that the mathematical models of Fisher, Haldane, and Wright had a direct influence on the synthesis architects like Dobzhansky, Mayr, Simpson, and Stebbins. See William B. Provine, "The Role of Mathematical Population Genetics in the Evolutionary Synthesis of the 1930s and 40s," *Studies in the History of Biology* 2 (1978): 167–92; William Provine, *Origins of Theoretical Population Genetics* (Chicago: University of Chicago Press, 2001 [1971]). Recently Provine has suggested that Mayr's fatal flaw as a historian and biologist came from his misunderstanding of genetics. William Provine, "Ernst Mayr: A Retrospective," *Trends in Ecology and Evolution* 20, no. 8 (2005): 411–13. Even in 2005, such a claim drew sharp and immediate criticism from evolutionary biologist Doug Futuyma, who wrote a letter defending Mayr. Douglas J. Futuyma, "Ernst Mayr, Genetics and Speciation," *Trends in Ecology and Evolution* 21, no. 1 (2006): 7–8.

115. In fact, Sewall Wright wrote to Stephen Jay Gould in 1981, suggesting that he had been deliberately excluded from the conference. Wright to Gould, 9 Feb 1981, Sewall Wright Papers, MS 60, American Philosophical Society, Philadelphia, PA, Series I: Correspondence, Folder Stephen Jay Gould.

the second would cover proximate approaches to the study of life.[116] Immediately after returning the final proofs of the first volume to the publisher, Mayr wrote again to Tinbergen, describing his historiographic intent in creating *The Growth of Biological Thought*:

> I vigorously defend the viewpoint that many of the theories and methodologies of the physical sciences are not sufficient for some of the processes of biology. What the physical scientists do not understand is that something can be completely consistent with the laws of physics and chemistry at the molecular level but that something that is controlled by genetic programs of information, something totally absent in the inanimate universe, can not be reduced to the laws of physics. I also vigorously promote the viewpoint that we naturalists have put a great deal of thought into biology which is necessary for a full understanding of the world of life.[117]

This is not to say that Mayr ignored genetics; he devoted almost two hundred pages to the study of "Variation and its Inheritance." As with the first two parts of the book, however, he began with Aristotle and wended his way slowly to the twentieth century. When he arrived at his final chapter on the chemical basis of inheritance, he noted that five or six books had already been written on the history of DNA research and so he would "touch only on the high spots and concentrate on the *biological* aspects of DNA research."[118] Arguing that biological thought in the early decades had been divided between the naturalists on the one hand and the experimentalists on the other, he asserted that the true payoff for genetics (as for diversity and evolution) came through its contribution to the modern synthesis.[119] Given Mayr's heartfelt commitment to ultimate causation in biological research, it is hardly surprising that he abandoned the second volume that he had planned to devote to the history of physiology, developmental biology, neurobiology, and the search for proximate causes in biological research.[120]

Reviews of *The Growth of Biological Thought* poured in, and almost all noted the battle lines Mayr drew between two antithetical research traditions: population thinking (key to evolutionary thought) and essentialism (key to the

116. Mayr, *Growth of Biological Thought* (ref. 93), vii–viii.

117. Mayr to Tinbergen, 26 Jan 1982, EMP, HUGFP 14.7, Folder Nikolaas Tinbergen 1980–82.

118. Mayr, *Growth of Biological Thought* (ref. 93), 811 (emphasis added).

119. Ibid., 566.

120. Ibid., vii–viii.

physical sciences).[121] In some cases, reviewers believed he had oversold his case and they doubted the longstanding rivalry Mayr presented—it too neatly situated molecular research within an older biological tradition that Mayr claimed was anything but "modern."[122] For example, Ian Tattersall's review in *American Anthropologist* noted that although Mayr promised "a history of the 'development of the ideas dominating modern biology,'" he delivered a far more idiosyncratic vision of "what Mayr personally regards as particularly important."[123] In fact, Tattersall continued, Mayr's "judgmental" voice throughout his book divided the cast of characters into a "long parade of heroes (for example Aristotle, Buffon, Darwin, Mayr) and villains (Plato, Descartes, most of the early experimental geneticists)."[124] Theoretical biologist John Maynard Smith's enthusiastic review nonetheless noted that it was "characteristic of Mayr's book that the emotion it arouses in me is a wish to argue with him, not about history, but about his scientific views."[125] In particular Maynard Smith took exception to Mayr's assertion that when mathematicians became interested in evolutionary theory they usually got it wrong or their views were irrelevant. Many reviews also noted the autobiographical flair Mayr imparted to his history. George Gaylord Simpson's review, for example, was even titled "Autobiology" and suggested that *Growth* was "in an unconventional and highly unusual way an autobiography. In it Mayr is seeking out, cleverly and successfully, the roots of his own accomplishments and opinions."[126] This did not detract from

121. Michael Ruse, "Admayration," *Quarterly Review of Biology* 60, no. 2 (1985): 183–92.

122. Mayr traced "essentialism" in biological thought back to Aristotle and Linnaeus. Recent scholarship has called this essentialism story into question and pointed to important work Mayr's argument performed in defending his own agenda. Mary P. Winsor, "Linnaeus' Biology Was Not Essentialist," *Annals of the Missouri Botanical Garden* 93, no. 1 (2006): 2–7, and "The Creation of the Essentialism Story: An Exercise in Metahistory," *History and Philosophy of the Life Sciences* 28, no. 2 (2006): 149–74; Staffan Müller-Wille, "Collection and Collation: Theory and Practice of Linnaean Botany," *Studies in History and Philosophy of Science, Part C. Studies in History and Philosophy of Biological and Biomedical Sciences* 38, no. 3 (2007): 541–62.

123. Ian Tattersall, "The Good, the Bad, and the Synthesis," *American Anthropologist*, New Series 86, no. 1 (1984): 86–90, on 87–88.

124. Philip Sloan's review also called attention to Mayr's tendency to use history judgmentally to separate historical actors by party labels. Philip Sloan, "Ernst Mayr on the History of Biology," *Journal of the History of Biology* 18, no. 1 (1985): 145–53, on 147.

125. John Maynard Smith, "Storming the Fortress," *New York Review of Books* 29, no. 8, 13 May 1982.

126. George Gaylord Simpson, "Autobiology," *Quarterly Review of Biology* 57, no. 4 (1982): 437–44, on 438; Jacques Roger and Michael Ghiselin, "More Maiorum (A Review Symposium)," *Isis* 74, no. 3 (1983): 405–13, on 410; see also Malcolm Jay Kottler, "A History of Biology: Diversity, Evolution, Inheritance," *Evolution* 37, no. 4 (1983): 868–72, and Niles Eldredge, "A Biological

Simpson's enjoyment of the book, however, and after summarizing many of its main highlights and addressing a few quibbles, he closed his review by heartily recommending the book to anyone interested in evolutionary theory. Of these reviewers, Michael Ruse was the most forthright in establishing his own argument. *Growth*, he suggested, "is not really a book about science at all. It is only accidentally a book about history . . . What Mayr is really trying to do is to persuade you of certain views of life, and to crush other views."[127] In the end, biologists read Mayr's *Growth of Biological Thought* with a keen sense of his professional and philosophical stakes in writing it.

Even so, many of the new histories of evolution that followed Mayr's history of the theory, as presented in both *The Evolutionary Synthesis* and *The Growth of Biological Thought*, were either imbued with the same philosophical assumptions as Mayr, or opposed to those assumptions. Evolutionary biologist Douglas Futuyma, for example, speculated that in dismissing the contributions of mathematical population geneticists (like Wright) to modern theories of evolution, Mayr was a victim of "that same lamentable rift between mathematical theoreticians and naturalists that delayed the arrival of the Modern Synthesis, and that persists still."[128] Yet despite this criticism, Futuyma's review burbles with enthusiasm and awe at the breadth and depth of Mayr's knowledge. With his historical writings, Mayr thus succeeded in setting the rules of the game for evolutionary history, even if other historians and philosophers disagreed with his version of that history. In doing so, Mayr also succeeded in providing organismic biology with a historiographic tradition that differed markedly from contemporary historical attention to the "molecularist" sciences.[129]

CONCLUSION

E. O. Wilson recalls that his views as an organismal biologist were "radicalized" by 1970. He "wanted a revolution" among young biologists interested

Urge to Oversimplify," review of *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*, by Ernst Mayr, *Philadelphia Inquirer*, 7 Nov 1982. Eldredge suggested that Mayr's autobiographical slant produced "bad" history—even though the "facts" were accurate, the interpretation was biased.

127. Ruse, "Admayration" (ref. 121), 190.

128. Douglas J. Futuyma, review of *The Growth of Biological Thought* by Ernst Mayr, *Science* 216, no. 4548 (1982): 842–44, on 843.

129. I have, for example, been unable to find a review of any of Mayr's historical books written by a molecular biologist.

in evolutionary theory.[130] Sure enough, as organismic biologists coalesced into a community with a coherent and unified past, this provided a ready target against which up-and-coming scientists could position themselves.[131] His hoped-for revolution came in many forms: mathematical ecology, paleobiology, and animal behavior. Wilson pointed to the loose cadre of biological theorists that began to form in the 1970s, from Lawrence Slobodkin, who founded the department of ecology and evolution at SUNY–Stony Brook in 1969, to Robert MacArthur, an early pioneer in theoretical population biology. We might easily add more names to the list such as John Maynard Smith, William Hamilton, and George Williams through the appropriation of game theory by biologists.[132] Recent historical attention to the emergence of paleobiology has illustrated how Stephen Jay Gould, Jack Sepkoski, and Tom Schoff challenged what they saw as a neo-Darwinian hegemony embodied in the theories of Dobzhansky, Mayr, and Simpson.[133] So even as organismal biologists struggled to unify themselves into a single defensive front, disunity welled up from within.

The political reordering of the American biological sciences during the 1960s and '70s forged a new professional identity for a particular group of scientists—as organismic biologists—with carefully calibrated philosophical, institutional, and historical foundations. It was also during these decades that the interests of biologists in the history of their own field encouraged historians and philosophers of science to pay attention to biology. As a result, the polarized dichotomies so characteristic and important to the organismic biologists of the 1960s and '70s were read back into the history of biology in some accounts, like Ernst Mayr's *Growth of Biological Thought* or, on a smaller scale, Simpson's depiction of the antipodal histories of molecular and organismic thought described in his article "The Crisis in Biology."[134]

130. Wilson, *Naturalist* (ref. 57), 232.

131. See Robert R. Sokal, "Another New Biology," *BioScience* 20, no. 3 (1970): 152–59, and the response, Illar Muul, Leigh van Valen, and Donald G. DeLisle, "What's New about the 'New Biology'?" *BioScience* 20, no. 12 (1970): 688–89.

132. Paul Erickson, "The Politics of Game Theory: Mathematics and Cold War Culture, 1944–1984" (PhD dissertation, University of Wisconsin–Madison, 2006).

133. David Sepkoski and Michael Ruse, eds., *The Paleobiological Revolution: Essays on the Growth of Modern Paleontology* (Chicago: University of Chicago Press, 2009), especially Joe Cain, "Ritual Patricide: Why Stephen Jay Gould Assassinated George Gaylord Simpson," 346–63, and David Sepkoski, "The Emergence of Paleobiology," 15–42; Léo F. Laporte, *George Gaylord Simpson: Paleontologist and Evolutionist* (New York: Columbia University Press, 2000).

134. Simpson, "Crisis in Biology" (ref. 32), 363–77.

Of course it comes as no surprise that the history of biology, as much as other histories, is political.[135] Yet if there was no necessary incommensurability between genetics and evolution, experimentalist and organismic methodologies, laboratory and field traditions, then the history of biology in the first half of the twentieth century might look radically different. This large-scale division of the history of the biological sciences is important because it has similarly divided the history of biology into two largely distinct historiographies. Recent scholarship is beginning to re-evaluate the dichotomy between "molecularist" laboratory-based biology and "organismic" field-based biology, especially evolutionary theory, within other times and other places.

A great many biological research programs sit at the interstices of these dichotomies, including animal behavior, invertebrate zoology, physiology, botany, developmental biology, and even eugenics. In his work on the history of ethology, for example, Richard Burkhardt has pointed to the diversity of places and practices devoted to studying animal behavior and the mutual collegiality of laboratory- and field-based biologists in the U.K. and Continental Europe.[136] The most systematic attempt to analyze the fruitful cross-pollination of experimentalists and naturalists in the early twentieth century is Robert Kohler's *Landscapes and Labscapes.*[137] In a recent essay entitled "The So-Called Eclipse of Darwinism," Mark Largent provocatively suggests that biologists' interest in evolutionary theory did not wane in the first decades of the twentieth century, but the myth of its eclipse allowed both biologists and historians to remove the history of eugenics from the mainstream history of biology.[138] Historians of

135. Abir-Am, "Essay Review" (ref. 5); Smocovitis, "1959 Darwin Centennial Celebration" (ref. 3). Joe Cain has raised even deeper concerns. If all of our histories can, and will, be used by scientists as a way of justifying their research agenda, he suggested, then the problem is not *if* history is political, but how to gauge the political consequences of our historical narratives. Cain, "Ritual Patricide" (ref. 133), 363.

136. Richard W. Burkhardt, Jr., *Patterns of Behavior: Konrad Lorenz, Niko Tinbergen, and the Founding of Ethology* (Chicago: University of Chicago Press, 2005), "Ethology's Ecologies," 447–84; Richard W. Burkhardt, Jr., "Ethology, Natural History, the Life Science, and the Problem of Place," *Journal of the History of Biology* 32, no. 3 (1999): 489–508. See also Gregory Radick, *The Simian Tongue: The Long Debate about Animal Language* (Chicago: University of Chicago Press, 2007).

137. Even Kohler takes the introgression of laboratory practice into naturalist traditions as requiring explanation and mostly disregards the influence of naturalist traditions on laboratory practice. Robert E. Kohler's *Landscapes and Labscapes: Exploring the Lab-Field Border in Biology* (Chicago: University of Chicago Press, 2002); Bruno J. Strasser, "GeneBank—Natural History in the 21st Century," *Science* 322 (2008): 537–38.

138. Mark Largent, "The So-Called Eclipse of Darwinism," in Cain and Ruse, eds., *Descended from Darwin* (ref. 15), 3–21; Diane Paul, *The Politics of Heredity: Essays on Eugenics, Biomedicine, and the Nature-Nurture Debate* (Albany, NY: SUNY Press, 1998).

botany in the twentieth century have also demonstrated substantial collaboration between botanists using molecularist techniques and those using more organismic methods.[139] By paying attention to these research traditions, historians have begun to rewrite the history of the life sciences in ways that describe the naturalist and experimentalist traditions as more collaborative and less antithetical than they seemed to organismic biologists in the 1960s.

Given the very limited ways in which one can generalize the political dynamics described in this paper, these new histories are especially important. Throughout this story, many participants in Mayr's conferences on the evolutionary synthesis, even his closest associates, like Dobzhansky and Simpson, objected to his philosophical or historical characterization of their own research, reacting to similar institutional and funding pressures in different ways. Mayr may have succeeded in protecting the future of organismic biology, but he did so by emphasizing deep divisions running through the biological sciences as a whole. By the close of the 1960s, Mayr's hopes for integrating all of biology under the banner of evolutionary theory had given way to a separate-but-equal approach to the organization of the modern biological sciences.

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139. Joel B. Hagen, "Experimentalists and Naturalists in Twentieth-Century Botany, 1920–1950," *Journal of the History of Biology* 17, no. 2 (1984): 249–70; Kim Kleinman, "Biosystematics and the Origin of Species: Edgar Anderson, W. H. Camp, and the Evolutionary Synthesis," in Cain and Ruse, eds., *Descended from Darwin* (ref. 15), 73–91; Vassiliki Betty Smocovitis, "The 'Plant *Drosophila*': E. B. Babcock, the Genus *Crepis*, and the Evolution of a Genetics Research Program at Berkeley, 1915–1947," *Historical Studies in the Natural Sciences* 39, no. 3 (2009): 300–55.