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INTRODUCTION

Special Issue Editor's Introduction: "Revisiting the Modern Synthesis"

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This special issue of the *Journal of the History of Biology* is devoted to revisiting the Modern Synthesis. This endeavor may seem odd. After all, a lot of work has been done by biologists, historians, and philosophers on the Modern Synthesis since the 1980s, including the landmark book *The Evolutionary Synthesis,* edited by Ernst Mayr and William Provine, which includes first-hand testimonies by protagonists of the Synthesis. Yet many studies of the Evolutionary Synthesis are not as systematic as this inaugural volume was. A number of works focus on leading figures, for example, on Julian Huxley (Cain 2010), Ernst Mayr (Junker 1996; Cain 1994), J. B. S. Haldane (Sarkar 2017), George Gaylord Simpson (Laporte 1991; Aronson 2002), Sewall Wright (Provine 1986), G. Ledyard Stebbins (Smocovitis 1997a, 2006). Others discuss particular topics, such as group selection, the species concept, classification, and population thinking (see Mallet 2010; Witteveen 2015; and Kimler 1986), or the formation of important societies, including the Society for the Study of Evolution and its precursor, the Society for the Study of Speciation (Smocovitis 1992, 1997b; Cain 1993, 2000, 2002). The major studies by Smocovitis and Cain interpret the rise of the Modern Synthesis within the general movement that transformed biology from a natural history discipline into a mathematized and experimental "science." Will Provine's decisive work on population genetics (2001) focused precisely on this transformation. Jean Gayon's (1998) philosophical history embraced a story that began with Darwin and traced the corroboration of the "hypothesis of natural selection." Yet, although this development was central to the Modern Synthesis, it did not explain the Synthesis itself.

Thus, a number of questions still remain unanswered, either because they have not been addressed or because different individuals assume very different answers. As Gayon says in his inaugural essay in this issue, we still do not know with

This special issue is dedicated to the memory of Jean Gayon.

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certainty answers to such fundamental questions as to *what*, *who*, *where*, and *when* the Modern Synthesis took place.

Scholars disagree, for example, about what precisely is meant by the name "Modern Synthesis." Is it something that is primarily theoretical, or does it designate an institutional or social event? The word *synthesis*, as Smocovitis (1994) argued, gestures towards unification and a general ideal of theoretical unity of science that logical positivists favored in the mid-twentieth century. Yet the effects of this Modern Synthesis might have been more visible at institutional and social levels than at the level of concepts—namely, in the creation of a professional society, journals, university chairs in evolutionary biology, and a network of biologists from various disciplines whose common interests were evolution and what it explains. In effect, the architects of the Synthesis disagreed regarding many of the crucial questions about evolution: the concept of species, units of selection and the levels at which selection acted, the nature and importance of interactions between levels of selection, the scope of selection, the rhythm at which it acted, etc. As Smocovitis (1992) aptly said, before the Synthesis, there was an "evolutionary theory" but not an "evolutionary biology," and the Synthesis allowed precisely this shift.

One could even question the unity of the Synthesis. Depew (2011) forcefully argued that there were two Syntheses, one located mainly in the UK and largely inspired by Fisher and later supported by biologists like John Maynard Smith, Richard Dawkins, and Alan Grafen; and the other centered in the USA led by such figures as Theodosius Dobzhansky, Sewall Wright, Ernst Mayr, George Gaylord Simpson, and, later, Stephen Jay Gould. The focus on adaptation was a hallmark of the former, while the latter was intrinsically more pluralist. Gould's (1983) well-known diagnostic of the "hardening" of the Synthesis, by pinpointing a shift toward a more adaptationist and gene-centered evolutionary biology, would thus appear as the takeover of evolutionary biology by the British tradition from the American. Thus, to borrow a useful phrase from Burian (1988), the Modern Synthesis is a "moving target" for the historian.

Yet this status contrasts with another perspective of the Synthesis, namely, the reference to the Synthesis within theoretical debates about what evolutionary biology should now be. In this discipline, it has become common to frame many issues regarding novel experiments, facts, or theories in terms of the necessity (or not) to move beyond the Modern Synthesis. This rhetoric has been moved to the foreground by several biologists, most of them proponents of Evo-Devo, under the label "extending the Synthesis." Since the publication of Massimo Pigliucci and Gerd Müller (eds.), *Evolution: The Extended Synthesis* (2010), intentionally accompanied by a re-edition of Julian Huxley's *Evolution: The Modern Synthesis* (1942)—the original source of the term the Modern Synthesis—many conceptual and theoretical questions debated by evolutionary biologists took the form of a controversy over the need to "rethink" the Synthesis. Indeed, widely-cited papers appeared in *Nature* in 2014 under the title "Does the Modern Synthesis Need a Rethink." Tenets of an alternative to the Modern Synthesis (Laland et al. 2014) were presented against the views of more orthodox-minded biologists, who think that the Synthesis is rich and wide enough to accommodate new findings about nongenetic inheritance, plasticity, developmental constraints, or niche construction (Wray et al. 2014). Independently

of the solution of this debate, it is worth highlighting the contrast between the role that the Modern Synthesis plays (in which it is taken for granted that the Synthesis provides a theoretical framework whose applicability to the new practices of biology is subject to challenge) and the prior account of the historical nature of the Synthesis as a moving target, much less well-defined than the (hardened) theory at stake in the scientific debate.

This contrast motivated the scholars who embarked on this project, whose outcome is the present special issue. It is all the more interesting that, from the beginning, the very notion of a Modern Synthesis was used by evolutionary biologists to persuade practitioners in a variety of disciplines that evolutionists shared many interests with those disciplines. Moreover, that notwithstanding the disciplinary differences involved, evolutionary projects and findings could be integrated with the work of biologists who worked in those disciplines and could help to resolve some of the difficulties encountered in those disciplines. Mayr and Provine's book (1980) was, indeed, at least as much an historical enquiry about the Synthesis as it was a theoretical stance regarding what evolutionary biology was (mainly according to Mayr) in its heyday. Thus, the reified use of the label *Modern Synthesis* is not exclusively proper to the present controversies, but rather occurred at the point when biologists began to interrogate it. Given the tension between a historical moving target and an objectified label, it seemed appropriate to revisit the various meanings ascribed to the Modern Synthesis.

This was the original intent of scholars who began to think about "Revisiting the Modern Synthesis" circa 2010. Jean Gayon, David Depew, Richard Burian, Edna Suárez Díaz, John Beatty, and I started to organize workshops and symposia in conferences in order to confront various perspectives on the Synthesis that deliberately avoided any commitment regarding current theoretical debates. Through those meetings and conferences, various views on the Synthesis were shared and confronted. Many colleagues joined us in various venues and shared their insights and results. The late Will Provine participated in the first workshop on the topic in Paris in 2010. Joe Cain, Betty Smocovitis, Roberta Millstein, Guillaume Lecointre, Alan Love, Pierre Dupuy, Paul Thomspon, Lisa Gannett, Franck Cezilly, Sophie Pécaud, Erika Milam, and Kevin Padian participated in events over the years. I would like to thank them here.

The Modus Operandi

After some time, this project crystallized around the following idea, mostly due to Jean Gayon. Given that many views coexist about where the Modern Synthesis started and what fields it covered, we should aim to be very open about these questions and consider less what the Modern Synthesis was than how it developed. Thus, we should look at the initial core of ideas about the Modern Synthesis identified in Huxley's 1942 book—namely, population genetics, which he considered as the foundation of such a synthesis—and then at the landmark volumes of Simpson (1949), Dobzhansky (1937), Stebbins (1950), and Mayr (1942) and how they expanded to embrace various fields and new directions and how these were transformed in the

process. Of special attention was the effect of the molecular revolution in genetics on various conceptions of the Synthesis at various times.

What provided the thread that structures our approach is the statement by Huxley, in the preface to *Evolution: The Modern Synthesis*: "The time is ripe for a rapid advance in our understanding of evolution. *Genetics, developmental physiology, ecology, systematics, paleontology, cytology, mathematical analysis*, have all provided new facts or new tools of research: The need today is *for a concerted attack and synthesis*. If this book contributes to such a synthetic point of view, I shall be well content" (1942, p. 8, my emphasis).

Hence, the idea of this special issue—which was kindly accepted in principle by this journal's previous editor Michael Dietrich, whom I warmly thank. Looking at how this "concerted attack" occurred, by analyzing how the fields named by Huxley were influenced and, in turn, changed by the Synthesis. The special issue itself, in addition to the various conferences and the workshops previously mentioned, stems from a conference held at the University of Chicago in November 2014 organized by Robert Richards, whom I want to thank here. Chance and authors' availability made the focus of this issue a bit different from the list of disciplines itemized by Huxley and even those included in the Chicago workshop. In the end, the papers on development and systematics could not be included.

The fields covered by the present special issue—analyzed under the perspective of how the Synthesis played, transformed, and/or appropriated those fields—include population genetics (Michel Veuille), behavioral science (Jean-Baptiste Grodwohl), ecology (Philippe Huneman), speciation (Anya Plutynski), and paleontology (David Sepkoski). Bookending these are papers that provide complementary perspectives on the entire issue. Jean Gayon's contribution situates the current state of questions about the Synthesis, summarizing some of the long-lasting thoughts he devoted to the nature of the Modern Synthesis since the appearance of his landmark volume, *Darwinism's Struggle for Survival* (1998). He argues for a reasonable skepticism regarding the idea that the Modern Synthesis was theoretical in nature. John Beatty's paper argues that the idea that natural selection was the genuinely creative process responsible for adaptive evolution, far from being a superfluous metaphor, may have provided the only core commitment of the Synthesis, distinguishing it from other evolutionary theories (e.g., orthogenetics, Mendelian genetics, etc.). We also received papers initially presented at the Chicago workshop that were published online in this journal before the present issue began to be assembled: one by Edna Suárez Díaz (2019) on molecular biology (a development that Huxley could not anticipate) and one by Maureen O'Malley (2018) on microbiology, which was also undeveloped at the time Huxley submitted his list of affected disciplines. These papers are in essence part of the same project and should ideally be read together with the others.

The aim to shed light on the Modern Synthesis was two-fold. First, putting together views of the Synthesis from different disciplinary perspectives—population genetics, ecology, speciation theory, etc.—provides us with a set of profiles of similar moving realities. Second, the juxtaposition of these views may leave readers with ways to think about general questions regarding the Synthesis: Was it one or several events? Was there a common core that appeared throughout all the various profiles? Ultimately,

we hope to have contributed to the theoretical question that excites biologists: about whether the Synthesis is finished or is still ongoing.

Much of what is written here uses or elaborates upon research already done, especially by the authors themselves. Part of the novelty of the project is this idea of collecting various profiles or perspectives on the same subject, with no initial intent to reduce it to a set of theoretical claims. Of course, each paper has been written with explicit attention to revisiting the Synthesis, and therefore of going beyond the state of the art in the historiography of the Synthesis in each field.

The reader may perhaps be confused by the absence of a common definition of the Synthesis presented in each paper. However, giving such a definition would have contradicted the character of the "moving target" of this Synthesis, which was part of our initial interrogation and triggered our intention to study the Synthesis along those lines. However, a minimal characterization is shared by the authors. The Synthesis started with the achievements of theoretical population geneticists, namely, R. A. Fisher, Sewell Wright, and J. B. S. Haldane and their seminal papers published between 1920 and 1932 (Fisher 1930; Wright 1922, 1931; Haldane 1932). But it really became a "Synthesis" following the publication of the landmark books by Huxley (1942) in the UK and by Dobzhansky (1937), Simpson (1944), Mayr (1942), and Stebbins (1950) in the US, all appearing in the "Columbia Biological Series" that was foundational for disciplining evolutionary biology. The bulk of the papers in this issue considers what happened to the Synthesis after this second phase, bracketing any a priori assumption about whether this still involved the Synthesis or represented something else. An overall result of this special issue is that there is no context-independent and field-independent answer to the latter question.

Historians appreciate differently this minimal, two-step characterization and the way the two steps add up. For instance, Beatty (1986) claims that the theoretical core of the Synthesis was population genetics (hence, the first step), but that the cited books provided observations and evidential support that conferred the theory its application domains as well as corroborations. On the other hand, Cain (2009) regards the Synthesis as having less theoretical substance after the 1930s and believes that what occurred was really a social movement in which a discipline was instituted and a network of researchers launched and maintained. These are two extreme characterizations, and yet both agree on the minimal idea that the Synthesis was not simply pure theory.

This minimal take on the Synthesis is shared by the authors of the papers in the present special issue. Yet, although their analyses may differ greatly, they tackle the same object. Even though they differ in placing an emphasis on one stage more than another in this classical, two-step schema, this does not affect the fact that they deal with the same Synthesis. Indeed, such differences are often justified by the different domains they treat.

The Content

The originality of the special issue is the focus on the Modern Synthesis over a quite long period, beginning in the early twentieth century and extending to recent time; for example, considering what occurred long after the 1960s (O'Malley's and

Grodwohl's papers) and even until 2000 (Plutynski's paper), or looking back at the 1930s (Veuille's and Huneman's papers).

Jean Gayon's paper, "The Modern Synthesis: Theoretical or Institutional Event?," frames the question of the status of the Synthesis as an object for historical investigation, based on the controversies and theoretical divides that paved the history of the Synthesis studies since Mayr and Provine's edited volume (1980), and on his own reflections on the topic. It serves as a conceptual introduction to the volume.

Michel Veuille's paper on population genetics questions the appropriation of the molecular turn and the neutral theory by the Synthesis in the post-1950 period, emphasizing how mathematical tools and methods developed by Sewall Wright or Gustave Malécot (1948) were then reactivated. It reconstructs how the neutral model has its roots in the effort of the theoretical population geneticist most often associated with natural selection, R. A. Fisher, and how the status of this model changed as a result of molecular data. He shows how the heyday of theoretical population genetics gained a new life via molecular perspectives on genomes and the acknowledgement of random processes at this level.

Anya Plutynski, in "Speciation Post Synthesis: 1960–2000," investigates what happened to the study of speciation after the consolidation of the Synthesis in the 1960s. It is well known that speciation was a major transversal question for the Synthesis biologists, as is attested by the fact that the ancestor of the Society for the Study of Evolution was the Society for the Study of Speciation. Plutynski shows how Theodosius Dobzhansky and Ernst Mayr's views, which framed research on speciation, were later refined and challenged. Following a reflective metaphor that sees the history of speciation studies as a story of divergence and diversification, she analyzes how various branches of research diverged from this core set while remaining in the same tree.

In considering the state of behavior studies, Jean-Baptiste Grodwohl first questions integration narratives, i.e., narratives framing the history of disciplines in terms of integration into or exclusion from the Synthesis. Drawing attention to an apparently typical episode of integration, during which some of the architects of the Synthesis (Mayr, Simpson) declared that behavior was part of the Synthesis, he argues that these claims had little immediate influence and should not be admitted uncritically. In describing later developments, more specifically the emergence of a discipline studying animal behavior in an evolutionary perspective, Grodwohl then emphasizes discontinuities with lines of thought and styles of working characteristic of the Synthesis. Although students of animal behavior used tools from population genetics, such as inclusive fitness, they developed an idiosyncratic use of them that was in several respects at odds with orthodox Synthesis thinking.

The paper by Philippe Huneman focuses on population and community ecology. He tells how the Modern Synthesis penetrated ecology by progressively infusing the idea of the key role of natural selection into the two main ecological questions of population regulation and species coexistence. The paper identifies several major steps in this history, each characterized by the positive role of some of the architects of the Synthesis, starting with Charles Elton's patronage by Huxley and ending with the rise of a mathematical theory of community ecology that is probably best exemplified by Robert MacArthur and E. O. Wilson's influential book on the theory of

island biogeography (1967). However, the paper concludes that no genuine homogeneity—defined by methodologies or the role of natural selection and the importance of genes—between the evolutionary Synthesis and ecology has been achieved.

In evaluating the impact of evolutionary biology on paleontology, David Sepkoski points out a paradox. While Simpson, a paleontologist, and his 1944 book undoubtedly played a key role in the rise of the Modern Synthesis, paleontologists often complained that the Synthesis left their discipline aside. This complaint was instrumental in attempts by Stephen Jay Gould, Niles Eldredge, David M. Raup, Steven Stanley, Jack Sepkoski, and others to turn paleontology into paleobiology and bring it to the "high table" of evolutionary biology. Elaborating on this paradox, and relying on his previous research, Sepkoski comes to a cautious and skeptical conclusion about the theoretical consistency of the Synthesis itself.

This skepticism echoes the doubts introduced by Gayon and Grodwohl in this issue. Interestingly, behavioral science and paleontology were two domains integrated in the Modern Synthesis, yet Grodwohl and Sepkoski, respectively, show major generational conflicts in those fields in the 1960s and 1970s. A key issue in this pervasive controversy is a shift in quantitative methods, and this is also shown in community ecology's mathematical modeling in the 1960s (e.g., Robert McArthur) addressed in Huneman's paper.

Another key aspect of the Synthesis in the 1960s and 1970s, illustrated by these papers, is the molecular turn. Historians have addressed extensively molecularization per se, but, inspired by Dietrich (1998), the present special issue shows how systematically the Modern Synthesis reordered itself around molecular data. This is at the center of Veuille's paper, but it also proves equally crucial in the history of speciation studies, as Plutynski shows, because electrophoresis allowed a novel and deeper understanding of species differences and speciation, which triggered the renewal of speciation biology after the 1970s. Suárez's paper demonstrates that Cold War funding was instrumental in pushing for the molecularization of population biology. This impacted another aspect of evolutionary biology in the 1970s, which is the object of O'Malley's paper, namely, the increasing theoretical role played by bacteriology in the formulation and testing of evolutionary hypotheses.

John Beatty, in Part 2 of "The Creativity of Natural Selection?," reflects on the use of the notion of creativity by architects of the Synthesis. Following from his earlier analysis (2016) of creativity during the period of the early reception of Darwin's thinking, especially by biometricians and Mendelians, Beatty shows that far from being a mere metaphor, *creativity* uncovers a deep conceptual argument that counters the Mendelians' idea that selection is just a filter or sieve, such that the rise of adaptive novelties in evolution is mostly due to variation. The long-lasting evolutionary discussion about the comparative roles of selection and variation in evolution and adaptation is thereby redefined. He claims that cumulative selection not only involves the elimination of the less fit, but also contributes to the production of the fittest. Notwithstanding all the known theoretical disagreements between Fisher, Wright, Dobzhansky, Mayr, and Simpson, Beatty convincingly argues that they all concurred in the overlooked claim that selection is creative.

It is striking that, while Beatty emphasizes the creativity of selection, his thesis is echoed by Veuille's paper, focusing on the effects of molecular biology on

population genetics. Drift finally took over the role of an alternative to Darwin's natural selection, which he saw as opposed to constancy of the species—hence a novel emphasis on a contrast between empty evolution (neutral change) and eventful evolution (selective change).

Overall, what these studies show—especially those concerning ecology and paleontology—is that different fields may have been transformed by the intervention of the Modern Synthesis's theories and concepts, but they often did not completely absorb the theoretical content of this Synthesis. As a result, they retained some conceptual autonomy, even if there was a considerable overlap in terms of people and institutions. The reader may find more continuity in the fields of genetics and speciation studies. In addition, Beatty's idea of the creativity of natural selection as a key commitment of the Modern Synthesis may provide a litmus test for deciding whether the Synthesis in various fields may be ongoing or simply remains an influence from the past. In any case, we hope that the present issue contributes to the question of deciding whether the Synthesis is still alive and well, or just belongs to the past.

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References

Aronson, J. 2002. "Molecules and Monkeys": George Gaylord Simpson and the Challenge of Molecular Evolution. *History and Philosophy of the Life Sciences* 24(3–4): 441–465.

Beatty, J. 1986. The Synthesis and the Synthetic Theory. In *Integrating Scientific Disciplines*, ed. W. Bechtel, pp. 125–136. The Hague, Netherlands: Nijhoff.

Beatty, J. 2016. "The Creativity of Natural Selection? Part I: Darwin, Darwinism, and the Mutationists. *Journal of the History of Biology* 49: 659.

Burian, R. 1988. Challenges to the Evolutionary Synthesis. *Evolutionary Biology* 23: 247–269.

Cain, J. 1993. Common Problems and Cooperative Solutions: Organizational Activities in Evolutionary Studies, 1937–1946. *Isis* 84: 1–25.

Cain, J. 1994. Ernst Mayr as Community Architect: Launching the Society for the Study of Evolution and the Journal Evolution. *Biology and Philosophy* 9: 387–427.

Cain, J. 2000. Towards a "Greater Degree of Integration": The Society for the Study of Speciation, 1939–1941. *British Journal for the History of Science* 33: 85–108.
Cain, J. 2002. Epistemic and Community Transition in American Evolutionary Studies: "The Committee on Common Problems of Genetics, Paleontology, and Systematics" (1942–1949). *Studies in History and Philosophy of Biological and Biomedical Sciences* 33(2): 283–313.
Cain, J. 2009. Rethinking the Synthesis Period in Evolutionary Studies. *Journal of the History Biology* 42: 62.
Cain, J. 2010. Julian Huxley, General Biology and the London Zoo, 1935–42. *Notes and Records of the Royal Society* 64(4): 359–378.
Depew, D. 2011. Adaptation as a Process: The Future of Darwinism and the Legacy of Theodosius Dobzhansky. *Studies in the History of Biology and the Biomedical Sciences* 42: 89–98.
Dietrich, M.R. 1998. Paradox and Persuasion: Negotiating the Place of Molecular Evolution within Evolutionary Biology. *Journal of the History of Biology* 31(1): 85–111.
Dobzhansky, Th. 1937. *Genetics and the Origin of Species*. New York: Columbia University Press.
Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Oxford, England: Clarendon Press.
Gayon, J. 1998. *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Natural Selection*. Cambridge: Cambridge University Press.
Gould, S.J. 1983. The Hardening of the Modern Synthesis. In *Dimensions of Darwinism; Themes and Counterthemes in Twentieth-Century Evolutionary Biology*, ed. Marjorie Grene, pp. 71–93. Cambridge: Cambridge University Press.
Haldane, J.B.S. 1932. *The Causes of Evolution*. London: Harper and Brothers.
Huxley, J. 1942. *Evolution: The Modern Synthesis*. Princeton, NJ: Princeton University Press.
Junker, T. 1996. Factors Shaping Ernst Mayr's Concepts in the History of Biology. *Journal of the History of Biology* 29(1): 29–77.
Kimler, W.C. 1986. Advantage, Adaptiveness, and Evolutionary Ecology. *Journal of the History of Biology* 19: 215–233.
Laland, K., T. Uller, M. Feldman, K. Sterelny, G.B. Müller, A. Moczek, E. Jablonka, and J. Odling-Smee. 2014. Does Evolutionary Theory Need a Rethink? Yes: Urgently. *Nature* 514: 161–164.
Laporte, L.F. 1991. George Gaylord Simpson as Mentor and Apologist for Paleoanthropology. *American Journal of Physical Anthropology* 84(1): 1–16.
Malécot, G. 1948. *Les Mathématiques de l'Hérédité*. Paris: Masson et Cie.
Mallet, J. 2010. Group Selection and the Development of the Biological Species Concept. *Philosophical Transactions of the Royal Society of London, B* 365(1547): 1853–1863.
Mayr, E. 1942. *Systematics and the Origin of Species from the Viewpoint of a Zoologist*. Cambridge, MA: Harvard University Press.
Mayr, E., and W.B. Provine (eds.). 1980. *The Evolutionary Synthesis. Perspectives on the Unification of Biology*. Cambridge, MA: Harvard University Press.
O'Malley, M.A. 2018. The Experimental Study of Bacterial Evolution and Its Implications for the Modern Synthesis of Evolutionary Biology. *Journal of the History of Biology* 51(2): 319–354.
Pigliucci, M., and G. Müller (eds.). 2010. *Evolution: The Extended Synthesis*. Cambridge, MA: MIT Press.
Provine, W. 1986. *Sewall Wright and Evolutionary Biology*. Chicago: University of Chicago Press.
Provine, W.B. 2001. *The Origins of Theoretical Population Genetics*. Chicago, IL: University of Chicago Press.
Sarkar, S. 2017. Haldane's The Causes of Evolution and the Modern Synthesis in Evolutionary Biology. *Journal of Genetics* 96(5): 753–763.
Simpson, G.G. 1944. *Tempo and Mode in Evolution*. New York: Columbia University Press.
Simpson, G.G. 1949. *The Meaning of Evolution: A Study of the History of Life and Its Signifcance for Man*. New Haven, CT: Yale University Press.
Smocovitis, V.B. 1992. Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology. *Journal of the History of Biology* 25: 1–65.
Smocovitis, V.B. 1994. Organizing Evolution: Founding the Society for the Study of Evolution (1939–1950). *Journal of the History of Biology* 27: 241–309.
Smocovitis, V. B. 1997a. G. Ledyard Stebbins, Jr. and the Evolutionary Synthesis (1924–1950). *American Journal of Botany* 84(12): 1625–1637.
Smocovitis, V.B. 1997b. *Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology*. Princeton, NJ: Princeton University Press.

Smocovitis, V.B. 2006. Keeping Up With Dobzhansky: G. Ledyard Stebbins, Jr., Plant Evolution, and the Evolutionary Synthesis. *History and Philosophy of the Life Sciences* 28(1): 9–47.
Stebbins, G.L. 1950. *Variations and Evolution in Plants*. New York: Columbia University Press.
Witteveen, J. 2015. '"A Temporary Oversimplification": Mayr, Simpson, Dobzhansky, and the Origins of the Typology/Population Dichotomy. Pt 1. *Studies of the History and Philosophy of the Biological and Biomedical Sciences* 54: 20–33.
Wray, G.A., H.E. Hoekster, D.J. Futuyma, R.E. Lenski, T.F.C. Mackay, D. Schluter, and J.E. Strassman. 2014. Does Evolutionary Theory Need a Rethink? No, All Is Well. *Nature* 514: 161–164.
Wright, S. 1922. 'Coefficients of Inbreeding and Relationship. *American Naturalist* 56: 330–338.
Wright, S. 1931. 'Evolution in Mendelian Populations. *Genetics* 16: 97–159.