Chapter 8
Little Evolution, BIG Evolution: Rethinking the History of Darwinism, Population Genetics, and the "Synthesis"

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> *Science commits suicide when she adopts a creed.*
> *—T. H. Huxley, quoted by Leo Berg (1926)*
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> *He bet on the wrong horse.*
> *—Theodosius Dobzhansky (1973)*

Abstract This chapter explores the history of the "micro-/macroevolution" distinction and its significance for the history of Darwinism, its "eclipse," and the "evolutionary synthesis." By noting how Darwin, Galton, DeVries, Fisher, Wright, Haldane, Chetverikov, Severtsov, Filipchenko, Dobzhansky, Goldschmidt, J. Huxley, Mayr, Simpson, Guyénot, Rensch, and others understood the distinction, and the language and arguments they used, the article chronicles the problems it posed for "synthesizing" diverse biological disciplines, and documents how the fundamental disagreements among them were successfully finessed by synthesis advocates. These findings force us to rethink the history of Darwinism, population genetics, and the evolutionary synthesis and their political, methodological, and national dimensions.

Keywords Charles Darwin · Darwinism · "Creative Darwinism" · "Eclipse" of Darwinism · Mendelism · Biometrics · Microevolution · Macroevolution · Megaevolution · Evolutionary synthesis · Population genetics · Paleontology · Systematics · Molecular biology · Theodosius Dobzhansky · Iurii Filipchenko ·

This chapter was written 30 years ago, in 1990; only the footnotes, the section on Julian Huxley (on the editor's prompting), and the "Apologia" at the end were written in 2020. Readers are advised to read that "Apologia" first.

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Julian Huxley · George Gaylord Simpson · Ernst Mayr · Richard Goldschmidt · Bernhard Rensch · A.N. Severtsov · Émile Guyénot · Leo Berg · Stephen Jay Gould

8.1 Did Population Genetics Save Darwinism?

The scientific field of population genetics arose early in the last century, sometime between 1905 and 1955. Historians quibble about exactly when: accounts date its inception variously from the Hardy-Weinberg law of 1908; a seminal note by R. A. Fisher in 1918; the mathematical papers of J. B. S. Haldane, Sewall Wright, and Ronald Fisher in the 1920s; the *Drosophila* field studies by Chetverikov's group, including Timoféeff-Ressovsky, 1925–1927; Theodosius Dobzhansky's classic 1937 book, *Genetics and the Origin of Species*; or the establishment of the distinct disciplinary status, legitimacy, and language of the field in the decade following World War II.[1]

If historians have disagreed about exactly when population genetics began, they have been remarkably unanimous about the historic importance of its achievement: according to well-established consensus, population genetics "saved" Darwinism and became the linchpin of modern evolutionary biology by making possible the so-called evolutionary synthesis, "synthetic theory of evolution," or "modern synthesis." Indeed, the overwhelming majority of works on the history of population genetics treat it almost entirely as part of the history of Darwinism and evolutionary theory. The "eclipse" of Darwinism during the period 1890–1930, including the "warfare" between Darwinism and Mendelism, has been thoroughly discussed in various books and articles by Bowler, Allen, and a host of British scholars. The rebirth of Darwinism in the evolutionary synthesis of the 1930s, 1940s, and 1950s has been explored in detail by Mayr, Provine, and many others. The role of population genetics in that rebirth has been the subject of important biographies of R. A. Fisher, J. B. S. Haldane, and Sewall Wright (Box 1978; Clark 1968; Provine 1971, 1986). The significance of Chetverikov and his students in initiating studies of the genetics of natural populations has also been the subject of important work (Adams 1968a, 1970, 1980a; Babkov 1985; Chetverikov 2002).

Alas, my own work has convinced me that much of this traditional view of the history of population genetics and its role in the evolutionary synthesis is fundamentally mistaken. Many of the details that I will deal with, of course, are well known to historians of the subject who work with original sources, and I think that

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[1] In my search for the origin of the term "population genetics," I asked a host of biologists and historians (including Ernst Mayr, N. W. Timoféeff-Ressovsky, G. G. Simpson, Will Provine, E. O. Wilson, and others) when, where, and by whom they thought the term was first used. All told me they did not know exactly, but guessed that it originated in the 1920s, and that Fisher, Wright, Haldane, and Chetverikov were the likeliest sources. Skimming all their works I could locate, however, the only thing I found was the phrase "the genetics of populations," along with other similar references to "the genetics of wheat," "the genetics of chickens," and so forth. There was nowhere the suggestion that it was a separate field, simply the genetic study of one kind of group or another. I was unable to find a single source using the term "population genetics" prior to Dobzhansky's 1937 book.

the factual details in my account will not be especially controversial. But the standard interpretation has all too often ignored these facts and their implications or else interpreted them in a Whiggish, wishful, or willful way. Properly understood, those facts demand a new interpretation of the history of Darwinism, population genetics, and the evolutionary synthesis.

My strategy will be, first, to present the standard historical view in brief. Then, I will set forth my alternate reading of that same history, redefining the central problem of Darwinism and the reasons for its "eclipse." Next, I will dwell on the founders of population genetics and the evolutionary synthesis in order to see how they dealt with that problem. Finally, I will suggest some alternate explanations for the triumph of the evolutionary synthesis.

8.2 Historiography: The Traditional View

The traditional history of population genetics and the evolutionary synthesis begins with Darwin and the difficulty in his theory uncovered by Fleeming Jenkin: the contemporary conception of heredity employed by Darwin, founded on continuous "blending" inheritance, renders impossible the accumulation of favorable, miniscule variations on which natural selection depends. In this view, Darwin's theory of natural selection was sound, but since he did not know genetics, his theory of heredity and variation was unsound; thus, the problem of the nature of heritable variation is often taken to be the central problem for Darwin's theory (Fisher 1930; Dobzhansky 1937, 1951a, b; Huxley 1942; Dunn 1965; Provine 1971; Allen 1975).

This traditional account sees the "eclipse of Darwinism" at the turn of the century as a consequence of this problem. According to an aphorism of the period, the trouble with Darwin's theory was that it explained the *survival* of the fittest, but not the *arrival* of the fittest. Hence, most biologists accepted the fact of evolution but contested its mechanism. New "experimental" theories attempting to explain the origin of favorable variations attracted scientific attention, notably the "mutation theory" of Hugo DeVries (1906). In Britain, this period witnessed the biometrician-Mendelian debate, traditionally interpreted as a disagreement over the kind of variation that could serve as a basis for evolution, with the biometricians emphasizing continuous variation, and the Mendelians discontinuous.

The usual historical account chronicles the resolution of this dispute through the integration of biometry, Mendelism, and Darwinism in the creation of a new field called "population genetics." Its creation is usually attributed to R. A. Fisher, J. B. S. Haldane, Sewall Wright, and Sergei Chetverikov, who demonstrated, beginning in 1918, that Mendelian particulate heredity destroys the objection to classic Darwinism of Fleeming Jenkin. In effect, so the story goes, these works reversed the theoretical situation. Before, biometricians and Mendelians considered Darwinism and Mendelism to be incompatible. Afterwards, Mendelism appeared to be almost a precondition for Darwinism and natural selection. The new perspective of the four founders was presented in their classic works: Chetverikov (1926), Fisher (1930), Wright (1931), and Haldane (1932).

At the same time, inspired by the works of Fisher and others, Sergei Chetverikov—a Russian butterfly specialist—initiated studies of the genetics of natural populations of *Drosophila* in 1925. In the 1930s, studies of the genetics of natural populations (sometimes called "experimental" or "ecological" population genetics) were developed by N. W. Timoféeff-Ressovsky (Berlin), N. P. Dubinin (Moscow), E. B. Ford (Oxford), and Th. Dobzhansky (Pasadena). Perhaps the most influential work in this vein was Dobzhansky's book *Genetics and the Origin of Species* (1937), which presented the new perspective in a general form accessible to biologists who, as a rule, did not read or understand complicated mathematics. Subsequent works by Julian Huxley (1940, 1942), Ernst Mayr (1944), G. G. Simpson (1944), Bernhard Rensch (1947, 1960), Ivan Schmalhausen (1949), G. Ledyard Stebbins (1950), and other biologists extended the "modern synthesis" to systematics, paleontology, botany, and other disciplines. As Mayr has characterized it, this synthesis involved the gradual acceptance of two conclusions: "gradual evolution can be explained in terms of small genetic changes ('mutations') and recombination, and the ordering of this genetic variation by natural selection; and the observed evolutionary phenomena, particularly macroevolutionary processes and speciation, can be explained in a manner that is consistent with the known genetic mechanisms" (Mayr 1980: 1).

This, in brief, is the classic view that has dominated the historiography of population genetics and evolutionary theory during the last century. Understandably, then, historians have occupied themselves with this unfolding logic, biographies of central figures who foresaw the synthesis, and with the explication of their successes. At times, the internal scientific logic has seemed so inexorable that historians have wondered how the synthesis could have taken so long to come about, concluding that personal and social factors must have played some role. For example, in his pioneering study *The Origins of Theoretical Population Genetics*, Provine noted that "the intense antagonisms generated by Bateson's dislike of Pearson and Weldon and vice versa contributed to a delay of more than a decade in the understanding that Mendelism and Darwinism were complementary," and concluded that "If Bateson and Pearson had collaborated instead of fought, population genetics would have gained a significantly earlier start" (Provine 1971: 177). Likewise, in comparative studies of the evolutionary synthesis in various countries, treatments of America and Britain emphasize that their biologists "got it right" because of their scientific insight and the lack of impeding factors, but authors dealing with Germany and France have looked to institutional, disciplinary, and social conditions to explain why their biologists seem to have lagged behind (Mayr and Provine 1980: 279–384).

This traditional history of population genetics is the one I learned and the one I taught for more than two decades. During the same period, however, my own research on Russian and European genetics and evolutionary theory began to raise some unsettling questions. How could it explain, for example, the many biologists in the 1920s and 1930s who understood and accepted genetics, population genetics, and Darwinism but who saw the relationship between them as problematic? Upon inspection, this view began to look suspiciously Whiggish. Considering the many ways history can be used to legitimate current approaches and agendas, I wondered about the origins of this triumphalist history. A preliminary survey revealed that its source may well be the founders of population genetics themselves: Chetverikov (1926), Fisher (1930), Wright (1931), and Haldane (1932) each introduced his classic work with a historical section outlining a variant of the traditional view stated above—namely, that the major problem with Darwin's theory centered on the nature of heritable variation and that this problem had now been put to rest. Did the founders frame their own contributions by defining the central problem of Darwinism to be the one they had already solved?

Upon investigation, it now appears that this traditional history is fundamentally misleading. In particular, I believe, it misstates a set of related issues: the central problem that Darwin addressed, the fundamental reason for the "eclipse" of his natural selection theory, the adequacy of the "evolutionary synthesis" in dealing with this central problem, and, ultimately, the reasons for its triumph. That central problem concerned the relationship between "little" evolution and "big" evolution, that is, between the origin of varieties, the origin of species, and the origin of higher taxa, or, more generally, between what came to be called "microevolution" and "macroevolution."

8.3 Darwin's Central Problem

In order to get from genetics (and population genetics) to evolution, one must see a link between the origin and character of intraspecific varieties and the origin and character of species and higher systematic categories (genus, family, order, etc.); and to do this, it is necessary to consider the variation within species (intraspecific) and the variation between species (interspecific) as qualitatively the same. If intraspecific variation and interspecific variation differ not in kind, but only in degree, then it is possible, by extension, to envision selection as the creator of new species. But if varieties are fundamentally different from species—if the fundamental character of intraspecific and interspecific variation is essentially different—then the effect of selection on a population cannot explain evolution. The species is the only link between the phenomena of the "selectionist" (breeder) and those of the "evolutionist," who traditionally deals with such larger problems as the sudden origin of radically new forms (vertebrates, or terrestrial vertebrates, for example), "progressive" evolution, and the appearance and elaboration in the fossil record of new structural plans and new systems of respiration, circulation, and mentality.

Darwin clearly recognized the importance of this link for his theory of natural selection—indeed, it explains the structure of his book (Darwin 1964). To establish his argument, he felt it necessary to demonstrate that a process analogous to the selection of domesticated plants and animals occurred under natural conditions and could create new species and higher taxa. Thus, Darwin begins the *Origin* with the chapter "Variation under Domestication," where he tries to establish the effects of conscious and unconscious selection on the creation of new varieties, and the probability of the original derivation of these domesticated varieties from natural species. Only after this does he discuss "variation under nature," the subject of his second chapter, where he tries to demonstrate that the traits used in systematic classification are arbitrary and that they are the same sort of traits whose differences are used to distinguish varieties. Only after these two chapters does he discuss the natural mechanism capable of replacing the breeder: that is, the struggle for existence and the resulting natural selection. But this relationship between varieties and species is so central to his argument that Darwin continually returns to it—in Chapters 5 ("Laws of Variation"), 6 ("Difficulties on Theory"), 7 ("Instinct"), 8 ("Hybridism"), 13 ("Mutual Affinities of Organic Beings: Morphology: Embryology: Rudimentary Organs"), and the final 14th chapter ("Recapitulation and Conclusion"). The book's only visual is in the "Natural Selection" chapter, analogous to a branching tree, which embodies Darwin's theory visually. There, he discusses it as a phylogeny; but an attentive reader will surely note that it could equally represent the origin of breeds and varieties within a single species.

Not only did Darwin understand this to be the central problem of his theory: so too did many of his critics. Indeed, although we have chosen to remember Fleeming Jenkin for his suggestion that blending inheritance would "swamp" new variations, his first critique centered on the implausibility of the view that varieties and species were comparable in their nature and origin and, in particular, that variations within a species could move outside of the range of variation delimiting that species (Jenkin 1867).

We must remember that Darwin advanced two distinct theories: evolution (or, as he called it, "descent with modification") and its mechanism ("natural selection").[2] Ironically, thanks largely to Darwin, by the time of the "eclipse" or "death" of Darwinism, the vast majority of biologists had come to accept his first theory (evolution), but not his second—not the validity of the theory of natural selection. Many of those who accepted the fact of evolution considered its cause or mechanism to be simply unknown. Others preferred orthogenetic theories, according to which the cause of evolution was entirely internal to the organism, because of the apparent directionality in long-term evolutionary trends. For still others, Lamarckian theories seemed more probable because of the perceived universal precision of adaptations in nature. For these scientists, there was little doubt that Darwin's theory could explain the success of the breeder in creating varieties; alas, the problem was rather the origin of species and higher taxa.[3]

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[2] What Darwin scholars know, but others seem not to, is that the word "evolution" is absent from the first edition of the *Origin*. (For the reason, see Richards, *The Meaning of Evolution*, 1992.) In addition, it expressed support for the inheritance of acquired characteristics and relied on it much more heavily in later editions.

[3] A popular anti-Darwinian book embracing Lamarckism during the "eclipse" was Peter Kropotkin's *Mutual Aid* (1902), which argued against intraspecific competition in animals, noting that in Siberia, herding and flocks helped protect species from both predation and environmental threats. However, during the "eclipse," undoubtedly the most influential and widely read anti-Darwinian book on evolution was French philosopher Henri Bergson's *L'Évolution créatrice* (1907), translated into English in 1911 as *Creative Evolution*. In place of natural selection, he

Nor did the so-called rediscovery of Mendel's laws change this situation. Even if there was considerable Mendelian variability within a species, what did that mean? It was still possible to conceive of the traits defining the species itself (and thus distinguishing it from other species) as the product of some Lamarckian mechanism, or of some internal "principle," or of some other factor or process as yet unknown—and this held as well for genera, families, and higher taxa. The relevance of Mendelism to the theory of natural selection depended on affirmative answers to two questions: (1) Are all the differences between species reducible to Mendelian genes? (2) Can the natural selection of Mendelian genes create new species and higher systematic categories?

To both of these questions, Hugo DeVries answered in the negative. Like Darwin, he regarded the relationship between varieties and species as the central problem and devoted one of his most influential books (*Species and Varieties: Their Origin by Mutation*) to the subject (DeVries 1906). For him, only "degressive" and "retrogressive" mutations could "Mendelize," but the mutations that established new species—the so-called "progressive" mutations—could not. DeVries's mutation theory was subsequently refuted by Lutz, Renner, and other researchers, but their work did not clarify the larger issue: as it turned out, these "progressive" mutations were not only not Mendelian, they were also not "progressive" in DeVries's sense—that is, they did not produce real, new species.

Similarly, although we have chosen to remember the work of Wilhelm Johannsen on "pure lines" for coining the term "gene," and his distinction between the so-called genotype and phenotype, we should remember that, for his contemporaries, it was most important as proof of the limited, purely intraspecific power of selection. Acting on a population, selection could alter the population to the limits of the genes it contained, but could not go beyond the species or populations limits: initially, selecting for the largest beans would increase their size to a point, but beyond that, further selection had no effect (Johannsen 1903, 1969). Even Francis Galton, the founder of both biometrics and eugenics, would have answered both of the key questions discussed above in the negative: Although his work on humans and peas amply demonstrated the impressive possibilities of selection within a species, he also demonstrated its limits to a species range of variability. Both discovering and emphasizing the so-called reversion to the mean (or, as he phrased it in 1886, "regression toward mediocrity"), he did not regard his own work as a clarification of the problem of the origin of species: to the contrary, he regarded their

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explained evolution by embracing both orthogenesis and Lamarckism, attributing its driving force to the *élan vital*, a "vital impetus" analogous to humanity's "natural creative impulse." The book was widely translated, read by millions, and one of the most popular books in the world in the early twentieth century. Both Dobzhansky and Mayr told me that they were much taken with it in their youth, and it inspired their choice of profession. Probably most (if not all) those who cultivated or opposed the "synthesis" of the same age cohort had read it. Of special interest for this paper was his notion of the "emergent properties" that appear in higher and higher forms of life (such as consciousness, intelligence, and language) that then govern and accelerate subsequent evolutionary progress.

origin as a result of some fundamentally different (as yet unknown) process (Galton 1930). Similarly, the biometrician-Mendelian debate actually centered not on the nature of heritable variation so much as on the question of whether intraspecific selection could produce a new species: the biometricians said yes, the Mendelians no.

One of the principal reasons for the eclipse of Darwinism, then, was the widespread conviction that Darwin's argument, based as it was on the role of selection in the origin of varieties, could not account for the origin of species or higher taxa. Many biologists simply did not believe that what delineated species and higher taxa was reducible to Mendelian genes, much less that the natural selection of such genes could create new species and higher taxa.

Darwin's book title had emphasized the origin of *species*, and he apparently believed that if natural selection could explain that, it could also explain the origin of genera, families, orders, and other higher taxa. As we shall see, from Darwin's day to the present, the "species" (and the now 26 different ways of defining them) has remained contested territory, and biologists have debated over exactly where the dividing line between "microevolution" and "macroevolution" should be drawn. Consistent throughout, however, has been the core problem of Darwin's "natural selection" theory, namely, its questionable relevance to what most scientists and the lay public have meant by "evolution."

8.4 The Perspective of the "Founders"

By 1930, however, four crucial biologists did seem to accept Darwin's views: Fisher, Wright, Haldane, and Chetverikov, the founders of population genetics. But how did these founders handle the central problem? How did they demonstrate that the differences between species were reducible to Mendelian genes? How did they demonstrate that the selection of Mendelian genes (which could create varieties) could also create species and higher taxa? How did they "save" Darwinism?

In his classic book, *The Genetical Theory of Natural Selection* (1930), Fisher did not treat this problem directly. Rather, his first chapter begins with a historical introduction, which is one of the earliest expositions of the "traditional view" of the history of population genetics that I have discussed above. Then Fisher uses that history to frame the following logic: there are a number of proposed theories of evolution, including the theory of natural selection; its only difficulty is the concept of blending heredity; the development of genetics invalidates the concept of blending heredity; all the other theories require blending heredity; thus, we must reject the other theories and accept the theory of natural selection. Let us quote from his book:

> The whole group of theories which ascribe to hypothetical physiological mechanisms, controlling the occurrence of mutations, a power of directing the course of evolution, must be set aside, once the blending theory of inheritance is abandoned. The sole surviving theory is that of Natural Selection, and it would appear impossible to avoid the conclusion that if any evolutionary phenomenon appears to be inexplicable on this theory, it must be accepted

> at present merely as one of the facts which in the present state of knowledge does seem inexplicable. (Fisher 1930: 21)

Note what he says here: either natural selection or we just don't yet know. Later, in his sixth chapter, there is a section entitled "Fission of Species," but there he simply assumes, without argument, that the morphological differences between species are the result of the accumulation of Mendelian mutations.

So much for Fisher—what of Sewall Wright? In his classic work "Evolution in Mendelian Populations" (1931), Wright addresses the question only in his introduction (which is also historical), concluding as follows: "As to gene mutation, observation of those which have occurred naturally ... reveals characteristics which seem as far as possible from those required for a directly adaptive evolutionary process. The conclusion nevertheless seems warranted by the present status of genetics that any theory of evolution must be based on the properties of Mendelian factors, and beyond this, must be concerned largely with the statistical situation in the species" (Wright 1931: 100–101). In his famous paper presented in 1932 at the Sixth International Congress of Genetics at Cornell, Wright notes that "It is only at the subfamily and family levels that clear-cut adaptive differences become the rule" and that "The principal evolutionary mechanism in the origin of species must thus be an essentially nonadaptive one" (Wright 1932). However, he cites this evidence not to show that varieties and species are essentially different (which was one plausible contemporary reading of that data), nor even to address the central question of their relationship, but simply to show the compatibility of such findings with his concept of "genetic drift."

J. B. S. Haldane raised the problem that Wright and Fisher evaded. In his book *The Causes of Evolution* (1932), which also begins with a historical introduction, Haldane defined evolution as "the descent from living beings in the past of other widely different living beings." Haldane acknowledges that selection within a population is not evolution proper: "Many would refuse to dignify the changes which man has effected in the dog as evolution," he notes (Haldane 1932: 4). Furthermore, he describes the purpose of his book as providing answers to a series of questions, among them "What is the nature of heritable differences within a species?" and "Are the differences between species of the same or of a different character?"

So far, so good—but what are his responses to these questions? After having described the character of variation within the species, Haldane reproduces a table that lists the color genes common to the mouse, the Norway rat, the black rat, the deer mouse, the cavy, the rabbit, the dog, the cat, and the ferret, noting that the Russian geneticist Nikolai Vavilov had obtained "similar results ... in cereals and other plants," as reported in *Nomogenesis* by the Russian ichthyologist, evolutionary theorist, and biogeographer Leo Berg (Haldane 1932: 65–66; Berg 1926). Then he makes the following observation: "Even the ferret and polecat, which have, perhaps erroneously, been placed in different genera, only differ as regards colour by a single gene. Of course the species and subspecies considered must differ by many other genes." His conclusion: "To sum up, interspecific differences are of the same nature as intervarietal" (Haldane 1932: 71, 82).

But hold a minute: the fact that certain species have certain genes in common, and differ in other genes, does not prove that the assortment of a species's genes constitutes the essence of its specificity. In fact, Leo Berg used Vavilov's data to demonstrate just the opposite! Berg considered the fact that very different species have Mendelian genes in common as evidence that species specificity was *not* determined by Mendelian genes, and there is contemporary evidence that Vavilov agreed (Berg 1926; Haldane 1932: 66, 79; Adams 1978b).[4] Thus, Haldane recognized the problem but did not resolve it. To be sure, if one accepted the proposition that varieties and species were qualitatively the same and that the only difference between species laid in their complement of Mendelian genes, all is in order; but if one didn't accept it, Haldane gives no convincing reasons to change one's mind.

The only one of the four founders of population genetics who directly confronted this central problem was Sergei Chetverikov. It was not difficult for him to do so: he had worked for 20 years as one of Russia's leading butterfly taxonomists. An entomologist and systematist, he actually first taught genetics in a course at Moscow University entitled "Theoretical Systematics." In Chetverikov's classic work of 1926, "On Certain Aspects of Evolution From the Viewpoint of Modern Genetics," the entire first section addressed the central problem. There, he argued that the traits determined by Mendelian genes in *Drosophila* (e.g., venation and wing structure) are the very same traits which are "fundamental in modern systematics for distinguishing higher systematic categories" (Chetverikov 1926: 9–10). Elsewhere in this same section, he mobilized his considerable knowledge of the systematics and classification of Diptera and Lepidoptera to make the same point.

Chetverikov's singularity derived not only from his specialty but also from his continental and specifically Russian setting. In this context, for both geneticists and evolutionists alike, it was far from self-evident that "microevolution" and "macroevolution" were the same sort of thing.

8.5 Macroevolution and Microevolution

This fact is well illustrated by the approach to the problem of the relation between genetics and Darwinism of two of Chetverikov's most brilliant contemporaries: Russia's most important evolutionist, Aleksei Severtsov, and its most important geneticist, Iurii Filipchenko.

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[4] When I was visiting Stephen Jay Gould one evening at his Cambridge home, he told me that he was much taken by this realization after reading my article on Vavilov, and used it as the basis (unattributed) for one of his popular science columns. (His personal thanks was the best apology for failing to mention my article as his source!) As for Haldane, he referred to Berg's work as "in my judgment the best anti-Darwinian book of this century" (p. 12).

Aleksei N. Severtsov (1866–1936) was the most distinguished Russian morphologist of his generation. Throughout his life, he regarded himself as a “pure” Darwinist. He embraced natural selection as sufficient, in principle, to explain all evolutionary phenomena. He rejected both Lamarckism and “autogenesis,” a term he coined to refer to all theories based on some hypothetical “internal principle.” In addition, during the 1920s and 1930s, he accepted the results of genetics and knew of the work of Chetverikov and his students. But in his final book, written 1935–1936 and published only after his death, he lamented that “Despite the brilliant achievements of hereditary theory, the results of genetic research have contributed almost nothing to the resolution of evolutionary questions” (Severtsov 1939: 80). Of course, for Severtsov (and most of his contemporaries),[5] “evolutionary questions” referred to the fundamental patterns in the history of life on earth: the appearance of new types, “retrogression,” “progressive evolution,” the origin of vertebrates, the conquest of land, the development of new and more complex forms of respiration, circulation, mentality, and, ultimately, of the psyche (Adams 1980b).

Although he was a geneticist rather than a morphologist, Iurii A. Filipchenko (1882–1930) was of exactly the same opinion. The leading advocate of the new “experimental zoology” in the Russian capital, and a biologist of broad profile and great influence, Filipchenko read many languages and had an encyclopedic command of world scientific literature, a knowledge he shared with his countrymen in many popular and technical books on diverse subjects—including biographies of Mendel and Galton; a history of evolutionary theories; textbooks on plant, animal, and human genetics; and books and pamphlets on wheat genetics, cattle breeding, and eugenics (Adams 1990c).

Like Severtsov, Filipchenko accepted evolution; but, unlike Severtsov, Filipchenko did not accept the theory of natural selection and did not believe that the specificity of categories above the species level was determined by Mendelian genes. In 1923 he argued that intraspecific variation was different in kind from traits characterizing genera and higher taxa, which exhibit “less variation” and “appear significantly earlier during individual development.” Unlike “traits characterizing the species,” for which “it is known exactly that their carriers are genes localized in the chromosomes of the sex cells . . . for the traits of a generic character, not only has no one proved this, but an entirely different proposition is considerably more likely, namely that they are present in entirely special carriers located, not in the nucleus, but in the plasm of the sex cells” (Filipchenko 1923: 213).

In 1927, in a German publication that he dedicated to the 70th birthday of Wilhelm Johannsen, Filipchenko codified this difference in language, distinguishing between two kinds of evolution: “microevolution” (*mikroevoliutsiia*—the evolution of biotypes, jordanons, and Linneons) and “macroevolution” (*makroevoliutsiia*—the

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[5] Indeed, as Nikolai Krementsov noted, almost a decade earlier, Russia’s foremost ornithologist M. A. Menzbir published the same sentiment in almost exactly the same words in two introductory articles in his Russian edition of *The Complete Collected Works of Charles Darwin* (Menzbir 1928, 1929).

evolution of higher systematic groups) (Filipchenko [Philiptschenko] 1927: 93–95). Elaborating this important distinction 2 years later, he declared:

> Thus, we consider that modern genetics, having established the nature of mutations and combinations, will undoubtedly throw light on the evolution of biotypes, jordanons, and Linneons. However, in addition to this, let us say, microevolution, there is the evolution of more major systematic groups, that is, macroevolution, and it undoubtedly lies beyond the purview of genetics, although it is the most interesting for evolutionary theory.
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> Given this state of affairs we must acknowledge that the resolution of the question of the factors of evolution of higher systematic groups, or our macroevolution, must proceed without reference to the facts of genetics. However nice it would be to be able to lean on them, it seems to us that they are useless for this purpose, because the question of the origin of higher systematic groups lies entirely outside of the field of investigation where genetics works. . . .
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> As a consequence, it is obvious that current and future evolutionary theory will undoubtedly resolve questions of the “origin of species” (and all lower subdivisions of species) differently from questions of the “origin of genera” (and all higher systematic units). As regards the former, it is impossible not to reckon with the conclusions of genetics, and given the current state of things there can hardly be any basis for disagreement. As regards the latter, to the contrary, at the present time we know very little that is precise, and this opens the field for the broadest speculation. (Filipchenko 1929: 260–261)

The authority of Filipchenko’s words derived from his unique status: not only was he Russia’s leading geneticist—the author of its most authoritative Russian textbooks, and an expert on the genetics of cattle, soft and hard wheats, and humans, its leading biometrician and its leading “Mendelist” and “Morganist”—he was also one of its leading authorities on evolutionary theory (Adams 1980a: 249).

Filipchenko’s views strongly influenced those of his most prominent protégé, Theodosius Dobzhansky. Dobzhansky worked closely with Filipchenko beginning in 1924 and came to idolize him. In 1927, thanks to Filipchenko’s nomination, Dobzhansky travelled to the United States to work in the laboratory of T. H. Morgan and, after the beginnings of Stalinism in the Soviet Union, he stayed for the rest of his life. The perspective of his teacher, Filipchenko, is evident in Dobzhansky’s evolutionary classic, *Genetics and the Origin of Species* (1937). In it, he co-opts his mentor’s neologisms to argue against Filipchenko’s reason for coining them.

How does Dobzhansky’s classic handle the central problem? In its introduction, Dobzhansky writes:

> Some writers have contended that evolution involves more than species formation, that macro- and micro-evolutionary changes may be distinguished. This may or may not be true; such a duality of the evolutionary process is by no means established. In any case, a geneticist has no choice but to confine himself to the micro-evolutionary phenomena that lie within reach of his method, and to see how much of evolution in general can be adequately understood on this basis. (Dobzhansky 1937: xi)

In the first chapter, he returns to the same subject:

> Experience seems to show, however, that there is no way toward an understanding of the mechanisms of macro-evolutionary changes, which require time on a geological scale, other than through a full comprehension of the micro-evolutionary processes observable within the span of a human lifetime and often controlled by man’s will. For this reason we are compelled at the present level of knowledge reluctantly to put a sign of equality between the

> mechanisms of macro- and micro-evolution, and, proceeding on this assumption, to push our investigations as far ahead as this working hypothesis will permit. (Dobzhansky 1937: 12)

And yet again, later in the book, he emphasizes that "No major evolutionary change is noticeable in most species of organisms within a human lifetime, hence the supposition that species have become what they are now through evolution by natural selection can be at best no more than a very probable inference" (Dobzhansky 1937: 151). Perhaps this is why Dobzhansky's own comparison of *Drosophila* species emphasized not their different or similar composition of Mendelian genes, but rather the differences in the number and configuration of their chromosomes.[6] In any case, similar language persists in the subsequent editions (Dobzhansky 1941, 1951a).

I was interested in the fact that, although Dobzhansky revered Filipchenko, and indeed got the words "microevolution" and "macroevolution" from him, he took an opposite stance in his book. During a weeklong interview of Dobzhansky at his camp in Yosemite shortly before he died, I raised the matter with "Doby" (a name he insisted on) and asked about his fundamental difference from Filipchenko over the "micro/macro" question. His response was surprising: he shrugged and said, almost indifferently, "He bet on the wrong horse."

Despite Dobzhansky's cautious language, however, his book undoubtedly played an important role in establishing "population genetics" as the core evolutionary discipline. One reason for its importance may be the way he used it to transform evolutionary discourse. In his first chapter, he declares categorically: "Since evolution is a change in the genetic composition of populations, the mechanisms of evolution constitute problems of population genetics" (Dobzhansky 1937: 11). Thus, in one great rhetorical finesse, he defined "evolution" as microevolutionary change, specifically a change in the genetic composition of populations; and then he made a daring claim of territoriality for a new field he called "population genetics" by declaring it to have primacy in dealing with the mechanism of evolution.[7] On this basis, the book subsequently asserted that the problem of the origin of species is resolved. In retrospect, it proved to be a brilliant and consequential move. Consider: When it is uncertain whether population genetics can illuminate what most people mean by "evolution," and evolution itself is under fundamentalist attack for being just a "theory," what to do? Dobzhansky's answer: kill two birds with one stone—*redefine* "evolution," and do so in a way that makes it a *proven fact*!

But certain European biologists were far from convinced. One in particular was Richard Goldschmidt (1878–1958), a very influential German biologist who was the director of the genetics department of the Kaiser Wilhelm Institute of Biology from

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[6] For information about Dobzhansky's increasingly cautious approach to the micro/macro issue, see Chap. 11.

[7] I was unable to find a single primary source using the term "population genetics" (as opposed to "the genetics of populations") prior to Dobzhansky's 1937 book, although he himself may well have used it in his own prior studies in the 1930s. Note that "the genetics of populations" is not the name of a field or discipline, whereas "population genetics" is.

1913 to 1935. A Jew, Goldschmidt emigrated to the United States in 1936 and became a professor at the University of California at Berkeley. Like many German zoologists, he regarded macroevolution as the central problem needing explanation. Confronted shortly after his arrival with Dobzhansky's book and the developing Anglo-American "synthesis," in 1940 Goldschmidt published a refutation entitled *The Material Basis of Evolution*. It begins with a scornful attack on the pretensions of this new "Darwinism":

> … I may challenge the adherents of the strictly Darwinian view, which we are discussing here, to try to explain the evolution of the following features by accumulation and selection of small mutants: hair in mammals, feathers in birds, segmentation of arthropods and vertebrates, the transformation of the gill arches in phylogeny including the aortic arches, muscles, nerves, etc.; further, teeth, shells of mollusks, ectoskeletons, compound eyes, blood circulation, alternation of generations, statocysts … poison apparatus of snakes, whalebone… Corresponding examples from plants could be given. (Goldschmidt 1940: 6–7)

The body of the book has two large divisions entitled "Microevolution" (pp. 8–183) and "Macroevolution" (pp. 184–395), terms he derived, he states, from Dobzhansky's 1937 book. The first part of his book concludes with the following words (printed in italics): "*Subspecies are actually, therefore, neither incipient species nor models for the origin of species. They are more or less diversified blind alleys within the species. The decisive step in evolution, the first step toward macroevolution, the step from one species to another, requires another evolutionary method than that of sheer accumulation of micromutations*" (Goldschmidt 1940: 183). At the time, Goldschmidt's book made him something of a pariah among those who were advancing the new "synthesis" (notably, Dobzhansky). Ironically, the Goldschmidt passages cited above could well have been penned by Dobzhansky's mentor, Filipchenko.

A second striking example of an unconvinced European biologist was the prominent French evolutionist Émile Guyénot. In his 1944 book, *L'Origine des Espèces*, and repeated in its updated 1964 American edition, Guyénot writes that "We know nothing positive about the genesis of groups larger than species." He continues: "As for the production of new types of organization, such as those characteristic of sub-kingdoms and the majority of classes, neither genetics nor embryology allows us a suspicion of the mechanism" (Guyénot 1964: 123). This leads him to distinguish between the "superficial evolution" treated by population genetics and the "evolution in depth" of the basic structural forms and plans of life, about which we know nothing. The book's final sentence declares, categorically, that "the great stages of evolution escape us entirely" (Guyénot 1964: 139). Thus, like Goldschmidt, Guyénot found population genetics and natural selection wholly inadequate to account for macroevolution, or, as he renamed it, "evolution in depth."

These examples suffice to demonstrate two interesting conclusions. First, for many biologists, population genetics did not prove the validity of Darwinism as a general theory of macroevolution. Second, whether as the study of intraspecific variation and selection or as the chronicling of genetic similarities and differences between species and/or higher taxa, population genetics was widely regarded, even by its strongest advocates, as being incapable in principle of dealing with the macroevolutionary problem.

8.6 Julian Huxley's "Modern Synthesis"

No treatment of this subject would be complete without including the works of the grandson of "Darwin's bulldog," T. H. Huxley, who gave the evolutionary "synthesis" its name. Historians are quite familiar with Julian S. Huxley's seminal contributions, notably *The New Systematics* (1940), which he edited, and *Evolution: The Modern Synthesis* (1942), which he authored. But I believe his story should begin more than a decade earlier (Adams 2000, 2004).

It was triggered by Huxley's younger friend and fellow Etonian, J. B. S. Haldane—not by his *The Causes of Evolution* (1932), but by his very well-known and controversial *Daedalus* (1924), in which he tweaks H. G. Wells for being out of touch. Admitting that "the very mention of the future suggests him," Haldane went on to declare him "a generation behind the time": "When his scientific ideas were formed, flying and radiotelegraphy, for example, were scientific problems, and the centre of scientific interest still lay in physics and chemistry. Now these are commercial problems, and I believe the center of scientific interest lies in biology" (Haldane 1924: 9–10).

Almost immediately thereafter, Wells set about rectifying this failing by drafting his son ("Gip," then a young zoologist at University College, London), and Julian Huxley (the grandson of his own teacher in the 1880s), to produce an encyclopedic popular book to be titled *The Science of Life*. Impressed by Wells's 1921 *Outline of History*, Huxley resigned from his academic job to undertake the project and devoted a whole chapter of his memoirs recalling the experience. There, he confirmed Haldane's criticism: Wells "had forgotten much of his biology, and what he remembered was by now old-fashioned—pre-Mendelian, with little study of animal behaviour or ecology. Thus the bulk of the scientific work would fall on my shoulders" (Huxley 1970: 155–6). As the multiple letters of the time quoted by Huxley demonstrate, almost all of the writing was done by Huxley, Gip, and two secretaries they hired, with Wells serving only as an active editor and handling the commercial side (Adams 2004).

After some 3 years of frenzied work, *The Science of Life* first appeared in three parts, each a long volume. One later edition of the work, published as a complete, single volume, was a very heavy tome comprised of 1510 pages of extremely tiny type (Wells et al. 1934)! In his memoirs, Huxley admitted that the experience had been frustrating and frenetic, but also admitted that it taught him a lot of biology.[8] Within its pages are views that would later fill Huxley's essays, popular writings, and

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[8] Will Provine once told me he regarded the work to be the "earliest complete presentation" of the evolutionary synthesis.

subsequent books, including his ideas on religion and “evolutionary humanism.” Nowhere do the words “microevolution” or “macroevolution” appear on its pages (although the massive volume covers both, in detail, and much more).

More than a decade later, in Huxley’s *Evolution: The Modern Synthesis* (1942), there is only one reference to those two terms in a page-long, not especially negative discussion of Goldschmidt’s 1940 book. Nor is there any other reference in the second edition (Huxley 1963, 1964). Nor does Huxley ever explicitly take a position on the “micro/macro” dispute, or discuss it.

Yet his book does reveal where he stands. On page 389 of both editions (1942, 1963/4), in a chapter on “Speciation, Evolution, and Taxonomy,” appears the following text[9]:

> The formation of many geographically isolated and most genetically isolated species is thus without any bearing upon the main processes of evolution. These latter, as we shall see in later chapters, consist in the development of new types endowed with mechanisms of higher all-round biological efficiency; in the adaptive radiation of these types to take advantage of all available types of environment and modes of life; in the colonization of new regions of the globe’s surface; in the tapping of new resources for exploitation; and in a more rapid turnover of the resources tapped.
>
> These major processes in evolution thus consist essentially in . . . a progressive increase of life’s control over and independence of the environment. Superimposed upon these processes, and having little or no bearing upon them, are the processes of species-formation we have just described which are the consequences of accidents in the environment or in the genetic machinery of life. Much of the minor systematic diversity to be observed in nature is irrelevant to the main course of evolution, a mere frill of variety superimposed upon its broad pattern. We may thus say that, while it is inevitable that life should be divided up into species, and that the broad processes of evolution should operate with species as units of organization, the number thus necessitated is far less than the number which actually exist. Species-formation constitutes one aspect of evolution; but a large fraction of it is in a sense an accident, a biological luxury, without bearing upon the major and continuing trends of the evolutionary process.

In other words, microevolution indeed can explain the origin of species, but that explanation has no bearing on macroevolution—evolution writ large, which follows different patterns and processes, and is progressive. Careful readers may note that these words closely resembled Goldschmidt’s.

This sustained position raises an interesting question: If, in Huxley’s views, microevolution (intraspecific variation and species formation) is different from and has no bearing on “evolution writ large,” then what exactly did he mean by “the modern synthesis”? To answer this question, we must look to the volume’s preface. Here he mentions that the book derived from an address he gave in 1936 titled *Natural Selection and Evolutionary Progress*, and explains:

> Even among professional zoologists the modern conception of natural selection and its mode of operation is quite different from that in Darwin’s day, but much of the research on which the changed outlook is based is so recent that the new ideas have not spread far. The idea of evolutionary progress, on the other hand, has been undeservedly neglected. Thus it seemed

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[9] My thanks to Richard Delisle for directing me to this page.

> to me valuable to attempt to give a broad account of the two concepts and their relation to each other.... The result is the present volume. (Huxley 1942: 7)

Later in the preface, he highlights his debt to Haldane's *The Causes of Evolution* (1932); praises the books by Dobzhansky (1937) and Goldschmidt (1940), claiming that, although his own book was already in proof when they appeared, "I have tried to take advantage of them where possible"; and notes his obvious debt to Fisher. He then concludes:

> 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 to-day is for concerted attack and synthesis. If this book contributes to such a synthetic point of view, I shall be well content. (Huxley 1942: 8)

Note that the "synthetic viewpoint" here is *aspirational*, not declarative, and privileges no single discipline over any other. His "synthesis" is not a doctrine but an ongoing process.

At the very opening of Chapter 1, "The Theory of Natural Selection," Huxley sets forth similar ideas, detailing the aspiration he is celebrating:

> Evolution may lay claim to be considered the most central and the most important of the problems of biology....
>
> Biology at the present time is embarking upon a phase of synthesis after a period in which new disciplines were taken up in turn and worked out in comparative isolation. Nowhere is this movement towards unification more likely to be valuable than in this many-sided topic of evolution; and already we are seeing the first-fruits in the re-animation of Darwinism.
>
> By Darwinism I imply that blend of induction and deduction which Darwin was the first to apply to the study of evolution. (Huxley 1942: 13)

After discussing historical disputes over the nature of variation and the so-called eclipse of Darwinism, he returns to his theme:

> Biology in the last twenty years, after a period in which new disciplines were taken up in turn and worked out in comparative isolation, has become a more unified science. It has embarked upon a period of synthesis, until to-day it no longer presents the spectacle of a number of semi-independent and largely contradictory sub-sciences, but is coming to rival the unity of older sciences like physics, in which advance in any one branch leads almost at once to advance in all other fields, and theory and experiment march hand-in-hand. As one chief result, there has been a rebirth of Darwinism....
>
> The Darwinism thus reborn is a modified Darwinism, since it must operate with facts unknown to Darwin; but it is still Darwinism in the sense that it aims at giving a naturalistic interpretation of evolution, and that its upholders, while constantly striving for more facts and more experimental results, do not, like some cautious spirits, reject the method of deduction...
>
> It is with this reborn Darwinism, this mutated phoenix risen from the ashes of the pyre kindled by men so unlike as Bateson and Bergson, that I propose to deal in succeeding chapters of this book. (Huxley 1942: 26–28)

What, then, is the synthesis that he is aspiring to? After a period when isolated subfields of biology, whose specialists were largely ignorant of one another's work, had caused an "eclipse" of Darwinism, he is seeing—and encouraging—that they all share their knowledge and contribute what they can to understanding evolution, and noting, indeed celebrating, that this was causing the rebirth of Darwinism. T. H. Huxley had famously served as "Darwin's bulldog"; his grandson now served as Darwinism's.

Dobzhansky had claimed "population genetics" to be the central evolutionary discipline; Severtsov had claimed that status for "morphology"; Mayr had claimed it for "systematics"; Simpson (as we shall see) claimed it for "paleontology." Unlike them, Huxley favored no single "evolutionary" science, but welcomed the diverse contributions of all who could contribute. Two decades later, he would preface the second edition of *Evolution: The Modern Synthesis* (1963, 1964) with a 39-page, unpaginated introduction that began: "In the twenty years since this book was first published, there has been an enormous volume of new work and new ideas on the subject of evolution.... The main fact to note is that the neo-Darwinian, synthetic, or integrative theory of evolution that I maintained in 1942 has gained many new adherents and may now be regarded as the established view." He then quickly surveyed and updated the new ideas and approaches to evolution coming from all fields (from geology to DNA). In that survey of 20 years of new work and ideas, he maintained the approach that he had taken throughout: that every field that could, should contribute equally; that all evolutionists should be in active communication and interaction; and that Darwinism in his sense had indeed been reborn.

Assemble all the relevant new information and tools from all fields, let each inform the others, celebrate the rebirth of Darwinism, and extend it to humans, society, and the future: that was the mission and approach he had undertaken for H. G. Wells in *The Science of Life*, and that continued to unfold throughout his popular essays and books, as Darwin's legatee, and as the first director of UNESCO. He might agree or disagree with certain theoretical assertions, but routinely sought to praise all contributors, functioning as a "welcoming evolutionary moderator." But Huxley saw no coupling between microevolution and macroevolution and sustained his broader vision of "evolutionary humanism" and evolutionary "progress" throughout. Given his communal role, his beliefs, and his goals, it may well have seemed to him counterproductive to get overtly involved in the "microevolution/macroevolution" spat, or even to use those words. Better to avoid that "issue" entirely.

8.7 Paleontology and "Macroevolution"

When, then, did the problem of macroevolution get resolved by the synthetic theory? The work usually credited with this is *Tempo and Mode in Evolution* (1944) by the American paleontologist George Gaylord Simpson. In light of this, we might find surprising what Simpson's book actually said. In his introduction, Simpson takes up the issue as a way of demonstrating the primacy of the paleontologist in handling it:

> ...Experimental biology in general and genetics in particular have the grave defect that they cannot reproduce the vast and complex horizontal extent of the natural environment and, particularly, the immense span of time in which population changes really occur. They may reveal what happens to a hundred rats in the course of ten years under fixed and simple conditions, but not what happened to a billion rats in the course of ten million years under the fluctuating conditions of earth history. Obviously, the latter problem is much more important. The work of geneticists on phenogenetics and still more on population genetics is almost meaningless unless it does have a bearing in this broader scene. Some students, not particularly paleontologists, conclude that it does not, that the phenomena revealed by experimental studies are relatively insignificant in evolution as a whole, that major problems cannot now be studied at all in the laboratory, and that macro-evolution differs qualitatively as well as quantitatively from the micro-evolution of the experimentalist. Here the geneticist must turn to the paleontologist, for only the paleontologist can hope to learn whether the principles determined in the laboratory are indeed valid in the larger field, whether additional principles must be invoked and, if so, what they are. (Simpson 1944: xvii)

In his third chapter ("Micro-evolution, Macro-evolution, and Mega-evolution"), Simpson takes up the "old but still vital problem of micro-evolution as opposed to macro-evolution," claiming in a footnote that "the terms are Goldschmidt's" (but failing to note that Goldschmidt credited Dobzhansky, who in turn got them from Filipchenko). This is how Simpson defines the terms:

> Micro-evolution involves mainly changes within potentially continuous populations, and there is little doubt that its materials are those revealed by genetic experimentation. Macro-evolution involves the rise and divergence of discontinuous groups, and it is still debatable whether it differs in kind or only in degree from micro-evolution. If the two proved to be basically different, the innumerable studies of micro-evolution would become relatively unimportant and would have minor value in the study of evolution as a whole. (Simpson 1944: 97)

He then claims, without evidence, that "the great majority of geneticists and zoologists believe that the distinction is only in degree and combination" (Simpson 1944: 97).

Simpson then handles the problem of "macroevolution" by redefining it. How surprising it is to a paleontologist, he notes, to find that the "higher categories" discussed in a monograph on macroevolution "are subgenera, at the highest possible evaluation, and indeed would be called 'species' by most paleontologists." He continues:

> If the term "macro-evolution" is applied to the rise of taxonomic groups that are at or near the minimum level of genetic discontinuity (species and genera), the large-scale evolution studied by the paleontologist might be called "mega-evolution" (a hybrid word, but so is "macro-evolution"). The assumption, as in Goldschmidt's work, that mega-evolution and macro-evolution are the same in all respects is no more justified than the assumption, so violently attacked by Goldschmidt and others, that micro-evolution and macro-evolution differ only in degree. (Simpson 1944: 98)

He then adds: "As will be shown, the paleontologist has more reason to believe in a qualitative distinction between macro-evolution and mega-evolution than in one between micro-evolution and macro-evolution." By substituting "megaevolution" for what many had meant by "macroevolution," was Simpson attempting a rhetorical finesse of his own?

Simpson's book, then, does not argue that what he calls "megaevolution" is explained by population genetics. Gould has rightly called the book a "consistency argument" (Gould 1980: 153–172). Even so, Simpson notes that "the facts are that many species and genera, indeed the majority, do appear suddenly in the record, differing sharply and in many ways from any earlier group, and that this appearance of discontinuity becomes more common the higher the level, until it is virtually universal as regards orders and all higher steps in the taxonomic hierarchy," and he adds: "The essentially paleontological problem is also of crucial interest for all other biologists, and, since there is such a conflict of opinion, nonpaleontologists may choose either to believe the authority who agrees with their prejudices or to discard the evidence as worthless" (Simpson 1944: 99). Indeed, Simpson warns the reader in his preface that "for almost every topic discussed in the following pages the data are insufficient" (Simpson 1944: xviii).

By the 1953 version of this book, published under the title *The Major Features of Evolution*, Simpson had added no new evidence for his dismissal of the macroevolutionary problem, but his tone had become more assured. Gould sees the changes from the 1944 version as evidence of "a much harder, much less generous, much more uncompromising line" which he terms the "hardening" of the synthesis (Gould 1980: 166). In his introduction, Simpson characterizes the "new and exciting idea" of his 1944 book as its attempt "to apply population genetics to interpretation of the fossil record, and conversely to check the broader validity of genetical theory and to extend its field by means of the fossil record," and then adds, with apparent satisfaction, that "This idea is now a commonplace" (Simpson 1953: ix).

He does not address the problem of macroevolution until the beginning of the 11th chapter, "Higher Categories." There, recalling his 1944 discussion about micro-, macro-, and megaevolution, Simpson remarks: "At present I am inclined to think that all three of these somewhat monstrous terminological innovations have served whatever purpose they may have had and that clarity might now be improved by abandoning them. . . ." Even so, he admits that "The study of evolution of higher categories, say for present purposes from families upward, does involve some of the most important problems of evolution," that there are "proper doubts as to whether the factors found experimentally in low-level evolution are those effective at high levels," and that "the absence of experimental control and the incompleteness of the fossil record make it difficult, although eventually not impossible, to draw final and decisive conclusions regarding widely variant, basic interpretations" (Simpson 1953: 339–340).

There is no doubt that Simpson's stand was important for the success of the synthesis. But what did Simpson offer by way of arguments or evidence to convince those otherwise predisposed? Clearly, for those continental biologists who, like Filipchenko, Goldschmidt, and Guyénot, believed that "big" (macro or mega) evolution was qualitatively different from microevolution, even Simpson's work gave them no reasons to change their opinion. In this connection, it is instructive to compare Simpson's treatment with that written by Severtsov only a few years earlier. Both held that the really important evolutionary issues are macroevolutionary ones; that studying the historical evolution of life on earth is the primary evolutionary science; that its data provide the ultimate test for theories concerning the evolutionary mechanism; that "autogenesis," "orthogenesis," "imminent principles," and neo-Lamarckism can be ruled out; and that Darwin's theory was essentially correct. Furthermore, both were aware of the results of population genetics and agreed that recent developments in genetics were brilliant and sound. But there agreement ended: Severtsov lamented the irrelevance of population genetics to evolutionary science, Simpson toasted its relevance. In the absence of evidence, Severtsov was not satisfied that population genetics provided all that was needed to explain macro- (or "mega-") evolution, whereas, in the absence of evidence, Simpson was.

A second figure credited with extending the evolutionary synthesis to the problem of macroevolution is the German morphologist Bernhard Rensch. His central contribution was a book written in Germany during the latter years of the war (Rensch 1947). In the introduction to the second edition, arranged by Dobzhansky and published in 1960 in America, Rensch addresses the central problem:

> It has become customary to distinguish between problems of 'macro-evolution' and 'micro-evolution'. As these two terms merely designate 'larger' and 'smaller' events without any clear borderline, and as they are linguistic mixtures of Greek and Latin roots, I prefer to use the terms 'infraspecific' and 'transspecific' evolution. Thus I hope to indicate a little more clearly the difference between those phylogenetic processes that occur within a species or lead to a new species and those that occur beyond the species limit and lead to new genera, families, and lesser divisions, and thus to new constructional types.
>
> At present, transspecific evolution is one of the central problems of evolutionary thinking. A number of biologists and paleontologists say that undirected mutation, selection, and isolation are not sufficient for a workable explanation or the causation of major phylogenetic phenomena and their regularity.... There can be no doubt that [the view that transspecific evolution is accounted for by infraspecific evolution] is somewhat 'unsatisfactory' to those who otherwise look entirely to the cause-and-effect principle in their research work. (Rensch 1960: 1–2)

Thus wrote one of the figures credited with extending the evolutionary synthesis to macroevolutionary problems—in 1960. Note also that, like Simpson, he chose to rename the dichotomy, in his case to "infraspecific" and "transspecific."[10]

When, then, was the problem of "big evolution" (whether called "macroevolution," "megaevolution," "transspecific evolution," or "evolution in depth") finally settled? The answer is, quite simply: It never has been. The appearance of the theory of punctuated equilibrium by Eldredge, Gould, and others, the attacks on the "hardening of the synthesis" by some punctuationalists, the republication of Goldschmidt's 1940 book with a highly flattering introduction—all are testimony

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[10] For a fuller explication of Simpson's evolving views and the philosophical underpinnings of Rensch's stance, see the chapters by Ochoa (Chap. 10) and Levit and Hossfield (Chap. 9). One paleontologist I spoke with remarked, "For my generation, Simpson was our god!" Others respected his work, but regarded him as something of an outlier, saw no possible relevance of population genetics to their work, didn't much care about or accept the "synthetic theory," and tried to ignore it. I asked one well-known paleontologist (who shall remain nameless) what the contributors to the synthesis (e.g., Dobzhansky, Mayr, Simpson, et al.) may have had in common, as he knew most of them. "I can tell you one thing they all had in common," he replied: "They were all sons-of-bitches."

that at least some of the persistent reservations concerning macroevolution remained (Goldschmidt 1982).[11]

8.8 Sociopolitical Dimensions of the Synthesis

Let us recapitulate by returning to Mayr's 1980 characterization of the evolutionary synthesis, in his introduction to the ultimate statement of its nature and history, which he thoughtfully orchestrated, and published when almost all of its other creators were dead (Mayr and Provine 1980). Claiming it was what Huxley had meant by the "modern synthesis," Mayr defined it as "the gradual acceptance of two conclusions: gradual evolution can be explained in terms of small genetic changes ("mutations") and recombination, and the ordering of this genetic variation by natural selection; and the observed evolutionary phenomena, particularly macroevolutionary processes and speciation, can be explained in a manner that is consistent with the known genetic mechanisms" (Mayr 1980: 1).

Parsing the rhetoric, the phrase "explained in a manner that is consistent with" seems carefully chosen. One cannot help but wonder precisely what it means. That no macroevolutionary phenomenon contradicts the validity of genetic findings? (No one claimed they did!) That macroevolutionary phenomena can be explained by the findings of population genetics? (Most professionals did not believe they could!) If it means the first, it is indisputable; if the second, it is more aspirational than descriptive. But a third possibility comes to mind: that the findings of population genetics and the "macroevolutionary" sciences are both valid and "consistent with" each other because they are unrelated—two entirely different subjects! (As we have seen, that is close to what Huxley actually meant!)

The traditional view is that population genetics, as developed by Fisher, Haldane, Wright, Dobzhansky, and others, played a central role in this synthesis. As to the first conclusion alluded to by Mayr—the one concerning "microevolution"—the role of population genetics was central. But, as we have seen, population genetics did not, did not claim to, and could not prove or even address the second conclusion concerning macroevolution—the reservation largely responsible for the "eclipse of Darwinism" in the first place. This simple but remarkable fact casts the evolutionary synthesis in a much different historical light. Mayr was, I think, correct in his observation that, at least in some disciplines and countries, many scientists gradually accepted that the old problem of macroevolution had been sufficiently resolved by the "evolutionary synthesis." In light of the foregoing analysis, we must ask where, how, and why it was gradually accepted.

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[11] At a conference at Penn in 1990, I sat in the second row behind Ernst Mayr when he was being chided by an advocate of punctuated equilibrium at the podium immediately in front of him, who contrasted his theory (looking directly at Mayr) with "evolution by creeps," eliciting audience laughter. Instantly, Mayr interrupted in a loud voice, shouting: "It's much better than evolution by jerks!" Note in the next paragraph Mayr's specification of "gradual evolution."

Geographically, in the 1920s and 1930s, the evolutionary synthesis was largely rejected in Germany and France and largely pursued and accepted in three countries: Britain, the United States, and the Soviet Union. At the height of popularity of the evolutionary synthesis, a new historical literature began to emerge, seeking to explain its international history, and account for its rejection in France and Germany. Interestingly, the conviction that microevolution and macroevolution were qualitatively different was one of the informing principles of that rejection. In a pathbreaking book, Jan Sapp painstakingly documented the development of ideas concerning cytoplasmic inheritance and made clear that, especially in France, many looked to it for the determinants that establish species and higher taxa (Sapp 1987). In a beautifully crafted article, Jonathon Harwood explored interwar Germany, demonstrating that the Grundstock hypothesis, the Plasmon theory, and research on Dauermodifikationen were aimed at this same macroevolutionary problem (Harwood 1985). In light of the inability of the synthesis to address macroevolution in any logically or evidentially compelling way, this rejection makes sense.

How, then, to explain its acceptance in Britain, America, and Russia? Let me offer some preliminary thoughts about the last two. Perhaps social and political factors played a role. In both countries, there were interesting, and in some respects opposite, "selection" pressures operating on both genetics and Darwinism that are worth sketching out.

In a book review (of *The Evolutionary Synthesis*) many years ago, Bentley Glass asked a pregnant question: Could it really be the case that creationism had no effect whatever on the development of the evolutionary synthesis in America? After the infamous Scopes Trial in 1926, the religious "creationist" opposition to Darwin denied the reality of evolution altogether, and the scientific arguments that they employed were based on the proposition that species and higher systematic categories were qualitatively different from intraspecific varieties and variations. (This, incidentally, remains a central tenet of so-called scientific creationism.) In this context, we should consider the utility of the definition of the word "evolution" deployed by Dobzhansky—"a change in the genetic composition of populations" (Dobzhansky 1937: 11). The self-evident conclusion is clear: evolution is not a "theory" but a demonstrable (indeed a demonstrated!) fact.

Perhaps in the United States, the battle to establish the validity of evolution in the face of creationist religious opposition solidified the identification between the general theory and those experimental researches that could demonstrate, and thereby "prove," that theory "as a fact." This situation may well have encouraged individual scientists to downplay their reservations about the macroevolutionary question in order to protect evolutionary biology as a whole: uncertainties about mechanism may have seemed less pressing when the validity of evolution itself was under attack, especially when those uncertainties were being deployed by the creationists to disprove evolution. Dobzhansky's extensive correspondence with one scientific creationist suggests that this criticism weighed, at least on this central figure in forging the evolutionary synthesis in America.[12] In Britain, Haldane had a similarly extensive correspondence of the same sort (Lunn and Haldane 1935).

In the Soviet Union, of course, there operated other forms of sociopolitical selection. While Darwinism was under religious attack in Coolidge's America, official Soviet ideology after the Bolshevik revolution was pro-Darwinist; indeed, Berg's *Nomogenesis* ran into trouble with the censor because of its explicit anti-Darwinian character. In Roosevelt's America, Darwinism continued under fundamentalist attack, but genetics was enthroned; in Stalin's Russia, just the opposite was true. After 1932, it was almost impossible to publish anything in Russia openly opposing Darwinism. In fact, in the late 1930s, "Darwinism" actually became a discipline with its own university departments. The nature of that "Darwinism," however, was hotly debated. Severtsov's student, Ivan Schmalhausen, assumed the chair of Darwinism at Moscow University, but I. I. Prezent, a philosophical ally of Lysenko, assumed the chair at Leningrad University. Lysenko and Prezent, of course, denied the validity of genetics and the reality of the gene altogether, and their so-called Creative Darwinism denied that intraspecific competition played any evolutionary role whatsoever. In 1948 and subsequent years, Lysenko gained Stalin's (and then Khrushchev's) support, and genetics was officially banned, going underground, until the partial rebirth of Soviet genetics following Khrushchev's ouster in 1964 (Adams 1978a). In this context, with Darwinism ideologically enthroned but genetics under attack as a "bourgeois science," it became important for Russian geneticists to be identified as "pure" Darwinists, and useful for them to demonstrate that their researches were not only consistent with Darwinism, but helped to demonstrate and reinforce it. Once again, sociopolitical pressures, albeit of a rather different character and intensity, may have encouraged scientific solidarity (Adams 1987, 1989a, 1991).

This brings us to the "triumph" of the synthesis in the late 1940s and the 1950s—when, as Stephen Jay Gould put it, the synthesis "hardened," the tone of its advocates changed from cautious and tentative to proud and assertive, and they came to treat doubters like Goldschmidt not as legitimate skeptics, but as heretical crackpots. What happened that might account for this remarkable difference between pre- and postwar attitudes and views?

One searches in vain for any scientific breakthrough concerning macroevolution that might account for this. The cause may reside again, at least in part, in sociopolitical factors—in the world war and its outcome. The victorious allies were Russia, Britain, and the United States—which just happened to be the countries where, for local reasons, the evolutionary synthesis had flourished; the "vanquished" countries were France and Germany, where that synthesis had been rejected by those who spent the war under Nazi rule. The war's end—and the revelation of Nazi atrocities in which German biologists participated—hardly predisposed Western biologists to

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[12] I have not read this unpublished correspondence, but Doby mentioned it in our 1973 interview, and Ron Numbers, a specialist in "science and religion" and the then editor of ISIS, had read the letters and emphasized their importance in a 1990 conversation.

take instructions from German biologists who resided in Germany throughout the Nazi period on matters of "race" (whether intraspecific varieties or subspecies) and its relationship to macroevolutionary progress. Later, of course, German biology was selectively relegitimated when particular works, such as that by Rensch (which seemed to more or less accept the new line), were published in English.

Furthermore, as John Beatty and subsequent researchers have demonstrated, the study of the Hiroshima victims and the fear of fallout led to the AEC's massive funding of population genetics. And this newly prestigious discipline, well financed because of its expertise on microevolution within human populations, was linked, as it happened, to a view that macroevolution was unproblematic.

I suspect, though, that in the United States (and possibly Britain), academic politics played a bigger role. So-called Big Science, which had developed earlier following the revolution in the USSR, took hold in the United States during World War II, and postwar America saw massive financial government support to science . . . especially to the right *kind* of science, useful science that was experimental, often conducted in laboratories, and addressed perceived immediate needs. Universities and faculties throughout the United States had to react swiftly to the new, powerful, emergent "molecular biology," and university administrators became addicted to government money. The situation in biology became especially tense, as my own professors explained to me (informally). For many years, in most universities, "molecular biology" was the winning, front-cutting-edge subject, and when "traditional" biologists retired, their replacements were almost always "molecular." The laboratory's promises and prestige overwhelmed field biologists, and all the more so after the Watson-Crick publication of the double helix structure of DNA in 1953.[13]

How could traditional biology survive? The "synthesis," it seems to me, served as a unifying, rallying call to save traditional biology under a new label parallel to its threatening rival: "evolutionary biology."[14] With "population genetics" at the core of

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[13] When I was in college at Harvard in the early 1960s, the only lights visible in the middle of the night were the molecular biology labs, working around the clock, trying to "break" the "genetic code." I remember sitting in a sparsely attended seminar taught by E. O. Wilson which was interrupted by dozens of students seeking the location of Watson's seminar on molecular biology, which, to the seven of us, seemed to clearly annoy him. Once the seminar began, Wilson announced: "Now, from the molecules of today, to the *biology* of tomorrow!"

[14] In this circumstance, "Darwinism" was increasingly a word to be avoided. (There is no "Einsteinism" or "Watson-Crickism.") The comparable "Darwinism" analogues (Aristotelianism, Platonism, Lamarckism, Freudianism, Marxism, Leninism, Mendelism) are terms referring to particular movements or traditions based on the thinking, philosophy, worldview, ideology, or theory of a single individual, not a field of inquiry or discipline identifying a generic subject. In the Soviet Union—the home of Marxism-Leninism—the field of "Darwinism" had not only scientific but also philosophical and ideological import. Although Huxley celebrated a "rebirth of Darwinism," he wisely characterized the scientific study of evolution as a "modern synthesis" created by many scientists from many fields. Given creationist opposition to evolution in the United States, any field called "Darwinism" was unlikely to be acceptable as a university department and could not successfully compete with "molecular biology" or attract government funding—hence the wisely crafted term "evolutionary biology." Throughout its history, the word "Darwinism" has been used in radically different ways, in different countries, by different people, for different purposes, to

this new incarnation, traditional biology was no longer a smorgasbord of zoological or botanical specialties focusing on different species groups or higher taxa (ichthyology, ornithology, herpetology, systematics, etc.). It was reborn as a "consensus" experimental, mathematical, laboratory discipline explaining and mastering evolution on every level (from flies, to crops, to people, and beyond).[15]

Soviet scientists had long since mastered such self-rebranding to satisfy the government that controlled their funding. Darwinism was part of official materialist ideological orthodoxy, so all scientists, regardless of specialty, became "Darwinists." When "eugenics" was officially condemned in 1930, all eugenics labs and journals were closed; but the network that supported it managed to create the new Soviet field of "medical genetics," and a large institute to study it, only 4 years later (Adams 1990a). When Stalin empowered Lysenko in 1948, condemning genetics as "idealist, capitalist science," and closing its labs and institutes, powerful physical scientists came to their rescue, and geneticists survived and continued their work in physics, chemistry, and mathematics institutes under different labels ("radiation biophysics," "cybernetics," "the chemistry of high molecular weight compounds," and so forth) (Adams 1978a, 2001). When Khrushchev was ousted in 1964, genetics was quickly re-established, only then publishing work that had been conducted during the interim (Adams 1978a).

American scientists also found similar ways of adapting to the new honeypot. Indeed, even before the government, the Carnegie and Rockefeller foundations had been supporting science selectively since the turn of the twentieth century. The establishment of "genetics" as an institutionalized field depended in these earlier decades on its ties with the popular, progressive "eugenics" promises of the day (and some of the earliest college textbooks in the field included both "eugenics" and "genetics" in their titles). Only after genetics had become firmly established and institutionalized did it distance itself from eugenics. After World War II, when "molecular biology" became the unifying new home for virologists, bacteriologists, organic chemists, biochemists, and so forth, "evolutionary biology" emerged as the consensus label for traditional biologists to move forward with "experimental

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mean different things. Most "Darwinists" of Darwin's day had all the same qualms as the "anti-Darwinians" of the early twentieth century. The last edition of Darwin's *Origin* (1872) embraced the inheritance of acquired characteristics, but three decades later, those who agreed with Darwin were branded "anti-Darwinian." The "Darwinism" of the Soviets ("Creative," and a part of their ideology!) was almost the complete inverse of the contemporary "Darwinism" of the "synthesis." Like other named "isms," the term's use is always problematic, because its meaning and utility are always granularly context dependent.

[15] When preparing this chapter for publication, I sent the final draft to several colleagues. On July 7, 2020, I received an email from Nikolai Krementsov, which I quote: "When I was working in APS, I saw a letter from Doby (from Brasil) to, if I remember correctly, Dunn, in which Doby complained that biology writ large . . . is going to be overshadowed by the molecular stuff . . . and that they should be doing something about it." Krementsov added that Doby made "a direct reference to AEC funding." "I can't remember, of course, the date or the exact wording . . . but the meaning of the letter supports very strongly your suggestion about coining "evolutionary biology" as a counterweight to "molecular [biology]."

evolution." Even so, those critical of the new consensus had a trying time.[16] Others managed to survive by rebranding their fields. When traditional "geology" began to seem an old-fashioned, field-based science most useful to energy companies, some departments managed to survive (and even prosper) by rebranding themselves as departments of "Environmental Studies" or "Climate Science."

Historians should distrust narratives that explain the acceptance of a theory in certain times and places "because it is right," while seeking social or political reasons for its rejection elsewhere. Explanatory symmetry must be demanded: acceptance and rejection both require explanation. No matter what we think is true right now, we have no way of knowing whether the future may see things differently. After all, alas, historically, what we now regard as truth has not always triumphed, and what were once dismissed as "mystical," "unscientific," "crackpot" ideas have turned out to be the basis for new sciences. Recall the times of "scientific consensus" that the earth could not move (the Copernican revolution!); that continents cannot move (plate tectonics!); that humans have 48 chromosomes (only in the late 1940s did we learn we only have 46); that water is scarce in the cosmos (it is almost everywhere!); and that all bodies far from the sun are frozen and dead (quite the contrary!)

I have tried to suggest some factors that may have contributed to the acceptance of the "evolutionary synthesis" in postwar America, Russia, and Britain, and against its acceptance elsewhere. Indeed, given the above, the temptation may be the opposite: Why did so many scientists come to accept (apparently) what could not be demonstrated or proved? Like many things in science that cannot be proved, but are accepted and believed, perhaps "normal science" requires a large dose of (dare I say it?) faith—or perhaps hope, dogged persistence, intuition, ideology, vision, self-interest, or pragmatism. Or, in Dobzhansky's words, perhaps scientists like to bet on the horse that seems to be winning.

8.9 Broader Implications

This new perspective on the history of evolutionary theory over the last century has historiographic implications. For one thing, it suggests that we need a new history of population genetics and raises questions about its origins. Traditionally, the rise of population genetics is viewed principally as the necessary and sufficient condition for the evolutionary synthesis. But if population genetics did not, did not claim to, and could not illuminate macroevolution, how are we to explain its development? Evidently, by looking at what, only later, came to be called microevolution. I would suggest that population genetics almost certainly developed in order to clarify, not

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[16] A renowned US embryologist told me he had spent his sabbatical doing research in Estonia, because the kind of embryology he was pursuing no longer existed in the United States, where all the newly hired embryologists for decades had made their departments entirely "molecular."

"natural selection," but "selection" in the original Darwinian sense: that is, plant breeding, animal breeding, and human breeding—eugenics.

Such a perspective helps to illuminate many features of its history that are sometimes ignored. For example, in his classic book of 12 chapters, Fisher devoted no less than five to eugenics (Fisher 1930: chapters 8–12). Sewall Wright has repeatedly emphasized the importance of animal breeding in the development of his own ideas and in the development of the discipline of population genetics generally (Wright 1967). Even Haldane, as the final chapter of his 1932 classic reveals, was motivated by his visionary hopes for human evolution in the distant future. (Haldane 1932: 144–170; Adams 2000). Finally, consider the origin of the term "gene pool," so central to population genetics. The term was coined by Dobzhansky in a popular paperback in 1946 against racism, and deployed in an evolutionary professional context in 1950, where it was used to define a "Mendelian population" (and thereby "evolution") (Dunn and Dobzhansky 1946; Dobzhansky1950, 1951b). But, as I have argued elsewhere, Dobzhansky probably translated the term from the Russian word *genofond* or "gene fund," used in the 1920s by his colleague Aleksandr Serebrovskii (Adams 1979). A eugenicist and a poultry breeder, Serebrovskii coined "gene fund" to dramatize his call for the creation of a "socialist" eugenic society in the Soviet Union and to analyze the movement of human tribes in Dagestan by studying their domesticated chickens (Adams 1990b).

These four examples suffice to show that the agricultural and eugenic dimensions of population genetics in the 1920s and the early 1930s were far from incidental. Literature on the history of eugenics has burgeoned, and work on the history of Mendelism and genetics in the United States, Britain, Russia, Sweden, and elsewhere has been making its agricultural and eugenic ties evident (Kimmelman 1983; Kimmelman and Paul 1988; Kevles 1985; Müller-Hill 1984, 1988; Weingart 1989; Adams 1989b).

I believe that this analysis may also have a broader historiographic implication for the discipline of the history of science itself. For many years, some historians and philosophers of science and technology have explored evolutionary approaches to their history, and some major historical books and articles have set forth the history of science and technology as a kind of Darwinian evolutionary process (Kuhn 1962; Adams 1968b, 1979; Nash 1967: 254–295; Fleming 1967; Gillespie 1968; Richards 1987; Hull 1988; Basalla 1988; Sapp 2003; many works by Donald Campbell and Stephen Toulmin). The utility of this approach—which owes more to Charles Darwin, Ernst Mach, and Alphonse de Candolle than to the much-maligned Herbert Spencer—is still far from generally accepted in our field.[17] But one need not follow

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[17] It will come as no surprise to historians of science that there are many dozens of metaphors, images, and narratives that have been used to model, characterize, or describe both the evolution of science writ large and of particular sciences. Those less impressed by the "Darwinian evolutionary model" than I am are invited to explore three other metaphors for the history of evolutionary biology in Esposito's interesting piece in this volume.

this approach to see suggestive parallels between the recent history of science and the earlier history of evolutionary biology.

We know that science has evolved, but how it has evolved remains open to dispute. Like orthogenesists of an earlier age, some historians have been sufficiently impressed with the diachronic continuities and long-term progressive trends in science to posit a largely autogenetic development of science, dominated by internal principles and factors. Like neo-Lamarckians, other historians have seen the manifold adaptations of science to its cultural, social, political, and economic milieux as proof that all science is socially constructed. In the 1960s and 1970s, like Darwinists, many historians saw the problem of the relation of the "internal" and "external" in the evolution of science as the central problem and challenge of our field. Some have sought to formulate "evolutionary epistemology." Others have attempted to understand the "ecology of knowledge" in supportive institutions and environments, the emergence of scientific "varieties" and "species" in the form of fields and disciplines, the role played by resources and institutional niches in their emergence, and the competition between fields for limited resources. There are those who emphasize the "macromutations" produced by minds of genius and others who emphasize the effects of intellectual and social selection on contemporary scientific variants.

Like biologists over the last century, then, we too speak of the evolution of science but dispute the mechanism. Microevolutionary studies of science of extreme granularity have proved remarkably fruitful in recent decades. Whether such studies can be used to address the "macroevolutionary" trends in the history of science and history more generally—among them the classic issues of scientific and technical progress and the origin and adaptive radiation of new kinds of natural knowledge—remains to be seen. There would seem to be a pervasive assumption, even in the absence of compelling demonstration, that they can. If history is anything to go by, the strong assertion of that certainty and its gradual acceptance—even without evidence—may, for a time, suffice.

Speaking of which, it has not escaped my attention that in the 1920s and 1930s, the tensions between the "little" and the "big" were not unique to evolutionary biology. In economics, for instance, as the field was transitioning from a social, philosophical subject into its modern, mathematical incarnation, issues regarding the relationship between "microeconomics" (and its "indifference curves") and "macroeconomics" (the overall economy, GDPs, and the like) were at the forefront: were they qualitatively different, or could the latter be explained or accounted for by the former? Likewise, in the new physics, there were the tensions between the almost infinitely "little" (governed by quantum mechanics—microphysics if you will) and the almost infinitely "big" (governed by relativity—macro- or mega-physics). These tensions vexed theoretical physicists, and do to this day, since the two are incompatible, and seemingly contradict one another. I suspect these are not the only examples. (What of the philosophers of science disputing "reductionism"? Or political "scientists" disputing the inherent tensions in federalism?)

Why, or how, would the same fundamental issue arise, apparently simultaneously and independently, in at least three such seemingly disparate fields? Could this striking parallelism be the result of selection? Or is it just a coincidence, resulting from the “microevolutionary” processes within each? Or, perhaps, are there broader “macroevolutionary” patterns, regularities, emergent properties, or trends in play? I do not know. But, in light of this history of the evolutionary synthesis, it seems a question well worth pondering.

Acknowledgments I wish to express my appreciation to Ronald Numbers, Richard Burian, John Beatty, Robert Richards, and Scott Gilbert, and most especially to Donald Forsdyke (Queens University), Nikolai Krementsov (University of Toronto), and Daniel Todes (The Johns Hopkins University), for their encouragement and support, as well as their advice and suggestions over the years for improving this chapter.

Apologia

This paper originated with a weeklong interview of Theodosius Dobzhansky in Mather Camp, Yosemite, during his field trip there in 1973, 2 years before his death. I had studied with Ernst Mayr, G. G. Simpson, and E. O. Wilson; I knew Russian, had just become an assistant professor, and was researching Doby’s firsthand experiences in Russia during the 1920s. Each day, after he had finished his field work, I would join him on his porch, chatting (and recording) one day in English, the next in Russian. His respect and admiration for his Leningrad mentor, Iurii Filipchenko, was almost worshipful: he pronounced his mentor the finest geneticist, biometrician, breeder, and evolutionary theorist in pre-revolutionary Russia and throughout the 1920s.

It was from his mentor that he adopted the microevolution, macroevolution terms that his 1937 book made standard. He also noted that his mentor had created those neologisms in 1927 (when Doby was his assistant and protégé) to distinguish varieties and species from genera and higher taxa, to make the case that, however useful in understanding the former, genetics could *not* illuminate the latter, namely, evolution. Yet, a decade later, now at Columbia, Dobzhansky deployed his mentor’s neologisms to argue just the opposite! I was puzzled, and I asked him, given his enormous respect for his mentor, how he accounted for the difference. I was expecting a technical answer. (Was it the influence of the Morgan School, his work with lady beetles, or some experience he had had?) Instead, he shrugged and said, almost indifferently, “He bet on the wrong horse.” (Doby was an inveterate horseback rider and was riding in Central Park when he was injured; he convalesced for weeks in hospital, where, at the urging of L. C. Dunn, he used the time to draft his 1937 classic book from memory, only adding bibliography when he could return to his office.)

“Bet”? “On the wrong horse?” I was startled, having never (in my innocence) thought of science as a “horse race” or a “betting” matter. That comment changed my perception. This was not a scientist who had been certain of his own approach, but rather someone who realized it might have gone either way, and chose the option that, if it turned out to be right, would both justify and empower his newly coined specialty, "population genetics." In subsequent years, I began to explore the evolutionary synthesis in greater detail, losing patience with triumphalist accounts, and gradually developing the views and evidence for this paper. Aside from teaching an annual lecture course on the history of evolutionary thought at the University of Pennsylvania, I broadened and deepened my understanding in preparation for various invited talks at universities, meetings, and other settings (at the University of Wisconsin, Ohio University, the University of Minnesota, Washington University in St. Louis, the University of Chicago, Virginia Tech, and Woods Hole, as well as in New York, Montreal, Paris, Geneva, Annecy, Uppsala, Oslo, Bergen, Moscow, Leningrad, Ischia, and the Naples Station).

I drafted the earliest variant of this article in the late 1980s. I had given a paper at a meeting in Paris and had to deliver it by a date certain in order to have it translated into French for publication—a deadline I missed. Calling on my high school French AP course, and consulting with various friends who were native speakers, I set about trying to translate my English ramblings but found that what seemed good academic English did not read well in French. So I set forth to create a new, short paper, in a more Cartesian, French style. It was subsequently published as "La génétique des populations était-elle une génétique évolutive?" in *Histoire de la génétique*, ed. Jean-Louis Fischer and W. H. Schneider (Paris: A.R.P.E.M., 1990), pp. 153–171.

Fearing that many of my colleagues could not (or would not) read French—and engrossed in the subject—I wrote a more extended English version of my thoughts. That was the initial draft of this paper. As I shared my findings with colleagues, I was strongly encouraged to prepare it for publication in ISIS by its editor and others. I came up with an almost final version, but ISIS changed management and it remained in the drawer. Over the years, various colleagues (including biologists, historians, and philosophers) encouraged me to find some way to make it publicly available, so they could cite it. After several such requests (a few quite insistent), I received an inquiry from Richard Delisle (whom, unfortunately, I have never met), sent him a copy of that paper, and he suggested publication in this volume. I have updated it here and there, and am grateful for the feedback and criticism from him and other colleagues, new and longstanding. Only the discussion of Julian Huxley is newly added, at the prompting of the editor. The standard references are from 1990; the footnotes provide new, 2020, relevant information, perspectives, comments, reflections, memories, and personal experiences.

I am neither a biologist nor a philosopher, but an historian. At one point, with the passage of time, I thought that by now, surely, many would have already realized the failings of the traditional view. But, alas, the "traditional" narrative still holds sway, as I learned when co-teaching a lecture course on the history of evolution just 4 years ago with a biologist who taught the introductory evolution course for the biology department. His take on "evolution" was all population genetics, equations, fitnesses, and claims of "evolution" (all intraspecific!), sprinkled with molecular biological updating, emphasizing Dobzhansky's claim that Darwinian evolution was not a theory, but a proven fact—and no mention whatsoever of higher taxa, fossils, extinctions, or the evolving history of life and nature on our planet. I am not so foolish as to think that my 1990 paper's publication will rectify the prevailing narrative, but I am very pleased to finally be able to make it available to interested colleagues and a broader readership.

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