Descended from Darwin

Insights into the History of Evolutionary Studies, 1900–1970

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Introduction

Michael Ruse

The time around the year 1959, the 150th anniversary of the birth of Charles Darwin and the 100th anniversary of the publication of his great book, *On the Origin of Species* (hereafter abbreviated as *Origin*), is a good point to mark the start of a really professional approach to the study and understanding of the history of evolutionary biology. In fact, the year before (1958) had seen the publication of one of the lasting major works of scholarship, a book by a Scandinavian student of English, A. Ellegård. To this day, *Darwin and the General Reader*, a detailed study of the reception of Darwin's ideas as shown in the periodical literature of the decade or so after the *Origin*, impresses by its thoroughness and sophisticated understanding of religious and other trends in the mid-Victorian era. Then in 1959 itself came *Darwin and the Darwinian Revolution*, by the American historian Gertrude Himmelfarb. In some ways, it is a strange book. The author does not much like her hero, probably a function of the fact that she was still very left-wing in her politics and saw (perhaps with some truth) that Darwin was a child of running-dog-lackey capitalism. One wonders why she wrote it. Perhaps it was part of a campaign to undermine the soft assumptions of mid-twentieth century capitalism. But despite Himmelfarb's somewhat negative attitude to Darwin and his achievements, the work itself is really serious and well researched, using hitherto unknown archival resources.

The Darwin year (1959) marked renewed interest in the first edition of the *Origin*, the beginning of a trend that sees the early *Origin* as being in many respects superior to later editions, especially the up-to-then-almost-invariably reprinted sixth edition (1872). This latter is a much revised work marred not just by the clumsiness of the multiple rewritings but also by Darwin's incorrect answers to important issues (like heredity), where his creative genius failed him, and his equally incorrect answers to important issues (like the age of the earth), where it was the creative genius of others and their wrong solutions that failed him. Serendipitously, one could start to judge the importance of which edition one was using thanks to the literary scholar Morse Peckham, who produced a still-exemplary variorum edition of the *Origin*, collating

all six editions. Ernst Mayr (Darwin, 1964) ensured a facsimile of the first edition was produced as part of this renewed attention. It has been in print ever since.

There were other signs that things were now starting to move forward, most particularly the beginning of the transcription and publication of Darwin's private notebooks that he kept when he was discovering natural selection in the crucial years of 1837, 1838, and 1839 (de Beer, 1960a, b, c, d; de Beer & Rowlands, 1961; de Beer, Rowlands, & Skramovsky, 1967). Darwin's two earlier versions of his theory, the 35-page *Sketch* of 1842 and the longer, 250-page *Essay* of 1844 were reprinted, making this material more easily available to scholars (Darwin & Wallace, 1958). Much credit must also go to Darwin's granddaughter Nora Barlow, who not only contributed considerable funds to the purchasing of manuscripts and letters and other material, thus making available essential data for use by scholars, but who herself worked assiduously to make available in the public domain valuable materials and sources. Particularly noteworthy was her edition of a full version of her grandfather's *Autobiography* (Darwin, 1958). The version that appeared in the *Life and Letters* soon after Darwin's death had been carefully and rather extensively bowdlerized by the concerned Darwin family. Now, for the first time, we could start to see the full extent of Darwin's thinking about sensitive topics like religion, not to mention his somewhat acerbic comments on some of his contemporaries (like Herbert Spencer).

The "Darwin industry" was off and running. But one should not think that it alone represented professional interest in the development of evolutionary thinking. People were starting to think and write about other important figures. Particularly noteworthy, for example, was a still-valuable study of Georges Cuvier by the Harvard student William Coleman (1964). This work was significant not only in its own right but also because it helped sensitize people to the fact that opponents of evolutionary ideas could be serious scientists, as well as showing that a temporal contextual study could offer good reasons why ideas that seem obvious and true to us today were not necessarily compelling in earlier times. Indeed, it might be necessary to show rather why it was that someone would commit himself or herself to ideas and thinking that, back then, were generally rejected for very good reasons. A few years later, another Harvard student, Richard Burkhardt (1977), was to do precisely that in his detailed and important study of Cuvier's evolutionary rival, Jean Baptiste de Lamarck.

Here is neither the time nor the place to go in detail into the development of historical studies of evolutionary ideas over the past 50 years. One thing that is worth noting—a fact still reflected by the background of one of the editors of this collection, as well as by the training of some of the contributors—is the extent to which the studies were enriched by the interest and activity of people whose primary professional commitments were to areas other than history. Thanks particularly to the influence of Thomas Kuhn's great work, *The Structure of Scientific Revolutions* (1962), many philosophers realized that they had to study the history of science in order to complete successfully their epistemological studies of scientific thinking. As a consequence, there was a steady stream of people who came to reap the benefits of the work of the historians and stayed to labor in the fields themselves. Later this stream was filled almost to overflowing by students from other fields, notably sociology and (more recently) areas like rhetoric. And of course, one should not forget scientists. Too often, before 1959 and after, scientists produce work on the history of their subjects that is midway between embarrassing and just plain awful. There are major exceptions, starting in

the history of evolutionary studies with Gavin de Beer, who was responsible for the opening of the Darwin evolutionary notebooks, and continuing down to the present. Martin Rudwick started as a paleontologist, producing an important monograph on the brachiopods, but then moved to the history of geology—a history that pays much attention to evolutionary questions—and for the past forty years has been the author of scholarship of the very highest level. (See, for example, Rudwick 1972, 1986.)

Then there was the indefatigable Stephen Jay Gould, who wrote many books, as well as a monthly column, "This View of Life," in *Natural History*. Gould wrote extensively on the history of evolutionary theory, touching at one time or another on nearly every major figure (and many minor ones), as well as holding forth on issues and events from the eighteenth century to the present. Much that he wrote was useful, informed, and always presented in a way that delighted for the style as much as for the content. He did, however, have agendas, most particularly a strong dislike of (what he would have called) ultra-adaptationism (and what many others would have thought was a sensible approach to evolutionary problems), something he felt led to all sorts of sins, scientific and social, most particularly a commitment to evolutionary progress (that, apart from anything else, he identified with racism). These driving forces could lead Gould to egregious lapses of scholarly objectivity, as for example when (on the flimsiest of evidence) he accused Father Pierre Teilhard de Chardin of being responsible for the Piltdown Hoax (Gould, 1980), thereby much downgrading Teilhard's status as a serious scientist (and in turn removing the twentieth-century's most enthusiastic progressionist from the realm of reasonable discourse). Overall, one has to cherish Gould's memory—works like *Wonderful Life* are masterpieces of popular writing, combining history with serious scientific themes—but (as we will suggest later) *caveat emptor*!

It does seem fair to say that, for many years, the study of the history of evolutionary theory was somewhat lopsided, not only in its almost laughable focus on one man, Charles Darwin, but also in the fact that when people moved from looking just at him, they tended to move backwards in time rather than forwards. I have already mentioned those who, even in the early years, were working on topics in the pre-Darwinian years. With very few exceptions, however, the post-Darwinian years were almost a closed book. There was some work on the history of genetics, although generally this was done for its own sake rather than as something that was to play a vital role in evolutionary understanding. One major exception to the rule was the Chicago-trained historian William Provine (1971), whose thesis (subsequently revised and published) was on the origins of the extension of Mendelian genetics to group situations and problems. Provine's work on the development of what came to be known as "population genetics" was careful, detailed, and deeply insightful about the ways in which in the 1930s evolutionary biology started to become a fully fledged area of professional study.

As is well known, subsequently Provine backed up his earlier work with a massive study of one of the key figures in evolutionary biology in the first half of the twentieth century. Provine's book on the American population geneticist Sewall Wright, and particularly his careful exploration of the ways in which Wright influenced the all-important, Russian-born American evolutionist Theodosius Dobzhansky, will long last as a testament to careful and revealing scholarship (Provine, 1986). On the American side at least, we now had a careful discussion of the so-called "evolutionary synthesis,"

as population genetics was fleshed out empirically, and scientists produced a working theory of evolutionary change. Naturally, the picture was still somewhat incomplete. Provine dealt only tangentially with other major figures, notably in America the very long-living taxonomist, ornithologist, and general evolutionist Ernst Mayr, the paleontologist George Gaylord Simpson, and the botanist G. Ledyard Stebbins. Even less attention was paid to the British. The great population geneticist Ronald A. Fisher was introduced more as an opponent of and foil to Wright, and his successors, such as Julian Huxley and E. B. Ford, got very slight treatment. But at least a major start had been made.

The German-born but long-time American resident Mayr, in fact, deserves special attention in his own right. He was not just a scientist but an extremely important editor and administrator, deeply interested in the history of his subject (Mayr, 1982). He wrote extensively, he encouraged even more extensively, and he organized prodigiously. All important was a series of conferences Mayr managed in the early 1970s, when he gathered together many of the then still-living major evolutionists of the early twentieth century, getting them to record their achievements and the reasons why they were able to do what they were able to do. Then, working with Provine, Mayr published the proceedings of these conferences, although scholars have discovered that even more valuable and revealing are the various (unpublished) questionnaires that Mayr devised to extract nuggets of information from key figures in the history of evolutionary theorizing (Mayr & Provine, 1980).[1]

As may be clear from the foregoing discussion, it would not be true to say that now the history of evolution is fully explored in a balanced fashion. Indeed, the collection that you have here is, in respects, part of an ongoing drive to flesh things out more evenly. Nevertheless, by the 1990s, things had so far advanced that those who thirst for overviews, trying to make sense of the big picture—what Stephen Jay Gould (2002) would have called macroevolution rather than microevolution (of concepts, not of organisms)—felt confident in trying to show overall themes or patterns in the history of evolutionary theorizing. Indeed, there are now two very different pictures being proposed. One by the prolific writer Peter Bowler (1996), who has produced studies covering the full range of evolution's history, sees a steady incremental picture. Clearly the work of Charles Darwin was a major breakthrough, but then there was much work to be done, work that led steadily but surely to the times in the last century when Darwinian selection and Mendelian genetics were brought together in one synthesis. The other picture, by one of the editors here (Ruse, 1996), sees things very differently. It is agreed that Darwin did make major contributions, but then it is argued that things stagnated. Not to put too fine a point on it, but from the point of view of science, the story of evolution after Darwin was an absolute disaster, with false hypotheses, faulty methodology, and yearnings for quasi-religious meanings. It was not until the 1930s that things really started again, and then it was necessary to ignore much that had gone before and to reach right back over the intervening studies to the *Origin* itself.

Time will tell whether there is truth to either of these rival pictures and whether the differences are simply a function of inadequate data or overblown imaginations. In the meantime, there is work to be done at the micro level, and the collection of articles published here represents this demand. We have brought together a number of the best younger scholars in the field of evolution history studies and invited them

to share their findings and interpretations. Focusing the subject a little, we tried to bracket the work within the first half of the twentieth century, and the spotlight is on work done by evolutionists in America and Britain. Although we did not make this a formal condition of contribution, we wanted in major respects to reflect the very important archival holdings of the American Philosophical Society, hoping thereby not only to draw attention to them but also to encourage other scholars to continue along this path.

The first of the four parts, Continuity and Breaks Across Generations, starts with Mark Largent's contribution (chapter 1), "The So-Called Eclipse of Darwinism." This chapter considers Vernon Kellogg's influential work *Darwinism Today* (1907) discussing whether, as was claimed by later evolutionists, the author is trying to sound the death knell for Darwinian—that is, natural-selection-based—evolutionary thinking, thereby contributing to the stagnation of really creative causal evolutionary thinking. Largent argues that this is not true of Kellogg's book, and thereby in some ways he challenges the Ruse interpretation of history that the time from the publication of the *Origin* to the coming of the synthesis in the 1930s was a Dark Age for evolutionary studies. Coincidentally, Largent also shows that evolutionists today often use historical examples in their own ways to buttress their own positions and to critique the positions of others.

Next by Juan Ilerbaig we have "'The View-Point of a Naturalist': American Field Zoologists and the Evolutionary Synthesis, 1900–1945" (chapter 2). This author likewise wants to challenge the claim that the time before the coming of the synthesis was a Dark Age for evolutionary studies, arguing that the work of field zoologists in the New World in the early part of the twentieth century was far more sophisticated and subtle and successful than later commentators, notably Ernst Mayr, allowed. Ilerbaig also raises questions about the relationships between studies done in nature and studies done in the laboratory. We shall be returning later to these questions.

Finally in this part, we have Andy Hammond's "J. B. S. Haldane, Holism, and Synthesis in Evolution" (chapter 3). The author stresses the importance of holistic philosophy throughout Haldane's intellectual career, meaning the extent to which Haldane consistently opposed a reductionistic approach to science. Hammond claims that this was especially true before Haldane became enthused with Marxism and thus ideologically committed to antireductionism. One important corollary of Hammond's chapter for those trying to make sense of evolution's history, especially those interested in the synthesis of Darwinian selection and Mendelian genetics, is how careful one must be not to assume all who were making the same moves were necessarily inspired by the same motives. Haldane is usually (with reason) linked with R. A. Fisher and Sewall Wright as one of the triumvirate developing population genetics (this is Provine's thesis). This may be true, but whether holism is important for anyone else is a very different question, and might lead us to see that although the similarities between the population geneticists outweigh the differences, one should nevertheless not ignore the differences.

We move next to the part: Emerging Narratives and Broader Themes. The first chapter here (chapter 4) is by Kim Kleinman: "Biosystematics and the Origin of Species: Edgar Anderson, W. H. Camp, and the Evolutionary Synthesis." Again we have a contribution that shows the devil is often in the details. The general opinion is that botany basically shows no great problems for or threats to the approaches

to evolutionary studies shown by the animal evolutionists and that the reason why the botanical contribution to the synthesis (by G. L. Stebbins, 1950) came later than those of Dobzhansky (fruit flies, 1937), Mayr (birds, 1942), and Simpson (fossils, mainly mammalian, 1944) was that the originally intended botanical participant Edgar Anderson was mentally unstable and unable to complete his contribution. Thus, Stebbins had to be recruited, necessarily later, and his contribution to the data followed the others. Kleinman suggests that the story might be more complex and that it would indeed help our understanding if we were to recognize that a plant is not an animal and that the effects of an organism obligatorally standing all of its life in one spot, rather than moving around, makes special adaptive demands. We should think about the essential differences between plants and animals before we start into overly quick generalizations about all organisms.

The next chapter (chapter 5) is an article by Joel B. Hagen: "Descended from Darwin? George Gaylord Simpson, Morris Goodman, and Primate Systematics." This fascinating chapter shows the full complexity of history. The synthesizers rightly saw themselves as revolutionaries. Yet, as Hagen proves, a revolutionary in one context may not be so revolutionary in another. Even as the synthesizers were making their case and their professional way, new threats were emerging—new threats to status and funds and students and the other goodies that make academic life so sweet. In the 1950s, molecular biology reared its ugly head and brushed aside the evolutionists. Hence, in response the synthesizers were little inclined to take seriously the claims of the molecular types, and when (in the early 1960s) molecular findings challenged traditional taxonomic divisions of humans and the higher apes, expectedly the major evolutionary authority, Simpson, fought back. Yet, as Hagen shows, apart from the fact that Simpson was wrong, both he and his opponents shared ideas and histories that got much distorted in the battle for supremacy.

Joe Cain's essay (chapter 6), "Ernst Mayr and the 'Biology of Birds,'" puts some much needed flesh on the bone of Ernst Mayr's description of himself as a "naturalist." Cain gives deeper meaning to the biographical fact that, although Mayr lived in New York, he was German born, bred, and educated and that this was always a dominant factor in his thinking. He shows Mayr was a determined reformer long before he focused his attention on evolutionary biology. These reforms shifted the emphasis from mere things to processes with conceptual underpinnings. This chapter helps explain why Mayr worked so tirelessly to interfere with the too-often uncritical way things were done in American zoology. The discussion of the "Biology of Birds" exhibition at the American Museum of Natural History is an important contribution of this chapter. It ties in nicely with recent interest by many historians of science in material culture and intellectual products other than books (for example, models, displays, and film). We could use many more studies of such things.

Gregory K. Davis, Michael R. Dietrich, and David K. Jacobs jointly author "Homeotic Mutants and the Assimilation of Developmental Genetics Into the Evolutionary Synthesis, 1915–1952" (chapter 7). One of the great puzzles in the history of evolutionary theory is the status of embryology. For Darwin in the *Origin*, it was of key importance, and he was very proud of his work in that direction. After the *Origin*, embryology became even more important, inasmuch as it was used by Ernst Haeckel and others to trace the history of life (phylogenies). But there was a backlash, for the life histories often were shown to be fictional. Hence, when the synthesizers arrived

they were little inclined to take embryology seriously, quite apart from the fact that, in the academic turf battles of the day (the generation before the threat from molecular biology), it was the embryologists who were dominant and who desired to adopt little of the synthesizers' genetics-based approach to evolution. Today, of course, evolutionary development ("evo-devo") is a major part of the evolutionary picture. The Davis-Dietrich-Jacobs chapter included in this collection begins the task of untangling the threads of twentieth-century studies of development to show how it is that something once despised and excluded can now be incorporated and favored. As always, the story started farther back in history than one might expect and involved personalities (in this case the German-born geneticist Richard Goldschmidt) whose existence and thinking in a somewhat contingent way shaped the ways in which things happened.

New Ideas and New Directions is the third part of this collection. The first essay in this part (chapter 8) is by Erika Milam: "'The Experimental Animal From the Naturalist's Point of View': Behavior and Evolution at the American Museum of Natural History, 1928–1954." One of the triumphs of evolutionary biology in the second half of the twentieth century was the way in which social behavior was brought into the evolutionary synthesis. So-called "sociobiology" is now a major part of the spectrum. There is, however, something of an inclination to think that, although Darwin in the *Origin* was very interested in social behavior, for various reasons—some reasonable, such as the difficulty of studying social behavior, and some unreasonable, such as the insecurities of social scientists and their unwillingness to let anyone else look at behavior—sociobiology was not at first brought into the synthesis but only added later. The brilliant models of W. D. Hamilton (1964a, b) are often taken to be the real starting point of progress. Milam shows, however, that this story can be only partially true and that in fact social behavior was being studied earlier. It is true that there were reasons why sociobiology did not flourish at once when the synthesis occurred, but by the 1950s real topics of lasting interest were engaging the attention of professional evolutionists.

David Sepkoski takes on "The 'Delayed Synthesis': Paleobiology in the 1970s" (chapter 9). Paleontology has always had an uneasy relationship with the rest of evolutionary studies. Although in the public mind it is the preeminent evolutionary area—"I believe [or do not believe] in evolution because of the fossils"—professionally it has a different status. Essentially, it can tell us little about causes, and hence those who can (like fruit flies specialists) tend to be condescending, and paleontologists in reply tend to be insecure and prickly. However, the synthesis did have a major paleontologist—George Gaylord Simpson—and he did labor to bring his subject into the synthesis. In the 1970s a new generation of paleontologists took over—a generation much better trained in genetics, ecology, mathematics, and similar fields—and they set about transforming their subject (Sepkoski & Ruse, 2008). Sepkoski's main question is whether these new "paleobiologists" (as they called themselves) continued in the Darwinian ways of the synthesizers or broke in radically new directions. His conclusion is that, for all that some (notably Stephen Jay Gould) claimed to be going off in new directions, in truth the new paleontology remained firmly within the synthesis. Sepkoski follows the historian-philosopher David Hull (1988) in stressing the importance of societies and journals for making the kinds of judgments he draws.

There are some tremendously important themes in John Ceccatti's contribution in chapter 10: "Natural Selection in the Field: Insecticide Resistance, Economic

Entomology, and the Evolutionary Synthesis, 1914–1951." Today it is a commonplace that diseases of various kinds require ever more potent methods of control and destruction. In the 1940s, a shot of penicillin would have cured the consequences of a night of incautious activity on the town. Today, it would prove quite ineffectual. The diseases in question have evolved sophisticated methods of resistance, and new remedies must therefore be sought. Ceccatti shows that evolving disease resistance (especially in plants) was known from the early part of the twentieth century and that it had a significant (if understated) role in the thinking of Theodosius Dobzhansky, especially as represented in his *Genetics and the Origin of Species* (1937). There was then feedback from the professional evolutionist to those working practically on the problems of disease control. Hovering over the whole discussion is the relationship between the person of theory and scholarship and the person of practical concerns, and more specifically the role of agriculture (especially as represented by the United States Department of Agriculture) in the formation of modern evolutionary biology. (As an aside, note that R. A. Fisher, J. B. S. Haldane, and Sewall Wright were all supported at crucial points in their careers by agricultural institutions.)

The final part of the book is Evolutionary Theory Meets Practice. Frederick R. Davis writes on "*Papilo Dardanus*: The Natural Animal From the Experimentalist's Point of View" (chapter 11). Mimicry has always been the jewel in the crown of Darwinian evolutionary biology. Shortly after the *Origin* was published, Henry Walter Bates (1962), the Amazonian traveling partner of (natural selection's codiscoverer) Alfred Russel Wallace, published an absolutely stunning chapter showing that the mimicry of certain species of tropical butterflies (where nonpoisonous kinds mimic poisonous kinds) can be readily explained by natural selection. The early Mendelians in their non-Darwinian zeal attacked this kind of explanation, arguing that it is all due to one-step mutations (Punnett, 1915). In reply, Fisher (1930) showed how indeed mimicry can work through selection, so long as one invokes modifier genes that trigger the effects of other genes. After the Second World War, the debate was rekindled between the non-Darwinian geneticist Richard Goldschmidt (1940) and the Darwinians of the E. B. Ford (1964) school of "ecological genetics," with members of the latter finally triumphing. The importance of Davis's chapter is not just that of showing the battle over selection with respect to mimicry but also (echoing a chapter in this collection) the key interplay that evolutionary biology has shown between those whose inclinations are always to look at organisms in the wild and those who readily (if not invariably) bring their subjects into the laboratory. Davis shows that these two approaches are not always opposed, and used properly can be very successfully complementary.

David Wÿss Rudge continues the study of mid-twentieth century British butterfly work in chapter 12, "H. B. D. Kettlewell's Research, 1934–1961: The Influence of J. W. Heslop Harrison." Kettlewell is an honored name in evolutionary studies. His work on industrial melanism in butterflies is generally taken to be (literally) a textbook example of how to do successful experimental studies of natural selection in action. Heslop Harrison to the contrary is reviled as a fraud and a cheat. Rudge shows in a detailed and penetrating study that, with respect to evolutionary work, Heslop Harrison is a more complex figure. In the early decades of the twentieth century it was he more than anyone who studied industrial melanism and its putative causes. Going somewhat against the tide, although certainly in a scientifically legitimate fashion,

he argued that pollutants caused new mutations and that this was the major causal factor involved rather than natural selection (spurred by the effects of pollution altering camouflage needs and strategies). This spurred the opposition of Britain's ardent selectionists, notably the Oxford biologist E. B. Ford, and the stage was then set for Kettlewell to take on Heslop Harrison in an attempt at refutation. At one level, Rudge shows nicely how scientific work is rarely if ever as clean cut and simple as textbooks suggest. At another level, he shows how influential mentors can direct and influence the course of scientific research.

Roberta L. Millstein is the author of chapter 13, "Concepts of Drift and Selection in 'The Great Snail Debate' of the 1950s and the Early 1960s." From the beginning of Darwinian evolutionary theory, starting with Thomas Henry Huxley (1859), there have long been critics of natural selection, especially as the chief mechanism of evolutionary change. The population geneticist Sewall Wright (1931, 1932) certainly gave selection an important role, but for the really creative moves in evolution he supposed that random facts, which he called "genetic drift," were all important. This was incorporated into what Wright called his "shifting balance theory of evolution," a vision of change that owed more to Herbert Spencer than to Charles Darwin (Ruse, 1996). In the early years after the synthesis in the 1930s, especially in America, drift was often given a major role, and much evolutionary change was thought nonadaptive. After the Second World War, the Ford school challenged this premise, and basing their studies on rural snails, A. J. Cain and P. H. Sheppard (1950, 1952, 1954) argued that much that had hitherto been thought nonadaptive (like shell color and pattern) was in fact tightly controlled by selection. Others, particularly on the continent, fought back and argued that drift is indeed important, and so the battle was waged. Showing the significance of the point made earlier about how philosophers have become engaged in the study of evolution's history, Millstein looks at this controversy, hoping thereby to throw more general light on the very natures and definitions of selection and drift. She argues that it is true that there are empirical questions here but that there are also matters of considerable conceptual importance not always recognized fully by the scientists at work on the issues.

Robert A. Skipper, Jr., in chapter 14, loops back and looks directly at the selectionist versus nonselectionist elements in the early population geneticists. His "Revisiting the Fisher-Wright Controversy" considers the questions that were raised by the two seminal thinkers, focusing especially on some of the issues of dominance (one gene masking the effects of its mate), where Fisher (1930) put everything down to natural selection and Wright (1931, 1932) wanted other factors to be significant. In a way, Skipper suggests that the differences were less contradictory, and more matters of emphasis about what level of explanation is truly significant. Fisher wanted selection-type explanations and Wright was more interested in physiological issues, these approaches reflecting what Mayr (1988) once described as a difference between ultimate (evolutionary) and proximate (physiological) explanations. Skipper (another philosopher) is keen to show that history can help to understand modern controversies, particularly one between two former colleagues at the University of Chicago, Jerry Coyne (Coyne, Barton, & Turelli, 1997) who is very critical of Wright's shifting balance theory and Michael Wade (Wade & Goodnight, 1998) who is an enthusiast for Wright's thinking. One will have to wait to see whether anyone will agree with

Skipper's ecumenical conclusion that every participant had some elements of truth and the final answer will demand acceptance of all views in some respects.

The final chapter of the collection (chapter 15) is by Mark E. Borrello: "Shifting Balance and Balancing Selection: A Group Selectionist's Interpretation of Wright and Dobzhansky." We have seen that one of the major achievements of the evolutionists working on social behavior in the years after the centenary of the *Origin* (1959) was to show how such behavior is open to explanation through natural selection. To do this, almost all of the seminal modelers argued that (following Darwin himself) the key to selection is that it works always for the benefit of the individual and never for the benefit of the group. (See, for instance, Williams, 1966.) It is the nature of philosophers to challenge the orthodox position, and much ink has been spilt in the past two decades and more on showing that individual selection is not necessarily as all important as the sociobiologists thought and that there must be a place for group selection—a position incidentally favored by Alfred Russel Wallace (Ruse, 1980).

Perhaps influenced by these philosophical speculations, Borrello has dug back into the history of the levels-of-selection debate, arguing that the chief group selectionist around the centenary, Vero Cooper Wynne-Edwards (1962), was not the crazed fool as presented by the sociobiologists, but a serious scientist who with reason thought that he stood firmly in the tradition of Wright and Dobzhansky. Borrello uses this fact to endorse a reading of the postsynthesis history of evolutionary theorizing proposed by Gould (1983). As noted above, Gould was no friend of adaptationism. Something he therefore had to explain was (noted earlier) how it was that in the years following the early work of the synthesizers (as for instance represented by the first edition, 1937, of Dobzhansky's *Genetics and the Origin of Species*), there was a move (in America) away from extreme enthusiasm for drift and toward a more adaptationist perspective. Gould argued this move to adaptationism (which was reflected by later editions of *Genetics and the Origin of Species*, especially the third in 1951) was less one driven rationally by evidence and reason, and more one of propaganda and rhetoric. A master of metaphor, Gould described this move as one of "hardening," with the intended unfortunate implications of a move made in a wrong direction—as in the hardening of the arteries or the hardening of Hitler's resolve after the weakness of Chamberlain at Munich. Again history will no doubt judge whether Borrello has chosen his allegiances wisely.[2]

Let us conclude this introduction by looking to the future. Fifty years have passed. We are now at 2009, the 200th anniversary of Darwin's birth and the 150th anniversary of the publication of the *Origin*. Without being smug, it is surely fair to say that the past 50 years have been incredibly productive. What then can we expect for the next 50 years? Or rather, let us frame the question like this: What should we now be doing to make the next 50 years as productive as the last 50? In the most obvious sense, we advocate more of what you have in this volume here. There is still a huge amount of work to be done, as is shown by the questions left dangling and unanswered by the chapters in this collection. Scholars must hit the books and go to the sources, especially to the archives held in Philadelphia and elsewhere. Also, of course, the history of evolutionary theory does not stand still, and more recent thinking needs scholarly study. Many of the most eminent and productive evolutionists of the second half of the twentieth century are now gone—Ernst Mayr, William Hamilton, John Maynard Smith, to name but three. The time has come to start looking at their work,

and the work of their contemporaries, in a detailed and professional way. Perhaps also given that so much communication today has gone from the more lasting paper to the more ephemeral electronic media, thought should be given to more work in the direction of recorded oral studies, so that the major thinkers of our time do not go unreported or with no significant traces.

It is very clearly the case that we need to broaden our gaze out from the Anglophone world, important though it is. We know, for instance, that Russian thinking about evolution has always been very important, and one suspects that in the field of population genetics major achievements lie waiting to be discovered or disseminated. The same is true in other countries, above all in Germany. As Joe Cain's chapter shows, some work is now being done in this direction, but nowhere near enough. We need full studies of German thinking before and after the major synthesizing moves that were made in England and America in the 1930s. Thanks to people like Stephen Jay Gould (Gould & Lewontin, 1979), we now realize that thinking in Germany and indeed elsewhere in many respects was very different from thinking in England and America. We need to learn more about its nature and its fruitfulness. In areas like systematics, given the influence of Willi Hennig, it is clear that German-style thinking was to be important, down to this day. In areas like paleontology, despite the champions both in the Old and the New Worlds, it is far less obvious that the German style of thinking was important and lasting. There are some indeed who think that it was a blight on a fast-moving area of science. Differences like these can only be resolved by intensive archival study.

It is important also that future historians of evolutionary biology try to balance the micro versus the macro. In a sense, the training and the profession push scholars toward the micro. One is told to cut one's intellectual teeth on detailed studies, almost always demanding archival explorations. One is also told to be wary of sweeping generalizations and to cherish exceptions and counter examples. In fact, there is even prejudice against the macro (Gould would have said in biology also) and a feeling that this is almost getting one into the realm of the popular—the coffee-table book and the television program. There is probably some truth in all of this. When you are racing through history, it is hard to be good at all of the details. As the distinguished social scientist Donald Campbell (1977) used to say about such efforts, one needs the nerve to be incompetent in many fields at once. Nevertheless, if one never does look up from the details and never tries to take in the whole landscape, one is missing something really important and exciting. One may indeed be doing one's micro studies a disservice as one fails to see that asking big questions often requires answers that come only from finding small solutions. Without the big questions, the focus will never be on finding the big answers, and that often means that the small questions will never be asked.

There is a lot of work to be done and there are lots of places to start looking, starting with the splendid archival holdings of the American Philosophical Society and elsewhere. We invite you to join in the hunt, and for inspiration we ask you to start by reading the splendid contributions to this collection.

NOTES

1. The American Philosophical Society has a holding of these questionnaires.
2. As a whole, the active British evolutionists never embraced drift, and followed Fisher in being adaptationists from the first. Apparently they were born with their circulatory systems in bad shape. As noted above, after the Second World War, Cain and Sheppard went after drift with a vengeance. But the move away from drift in America had already started. By the early 1940s, Dobzhansky was thinking that the move to adaptationism was a reasonable scientific response to discoveries that fruit fly chromosome patterns cycle in predictable patterns, suggesting selection, and not at all at random, suggesting drift. See Lewontin, Moore, Provine, & Wallace, 1981, for the key documents and Ruse, 1999, for more detailed discussion of Dobzhansky's reasons for change.

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