The Paleobiological Revolution

ESSAYS ON THE GROWTH OF MODERN PALEONTOLOGY

Edited by
David Sepkoski and Michael Ruse

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INTRODUCTION

Paleontology at the High Table

David Sepkoski and Michael Ruse

In 1984, Stephen Jay Gould's Tanner Lectures at Cambridge University presented an overview of the major advancements paleontology had made since he and Niles Eldredge first unveiled their infamous theory of punctuated equilibrium in 1972. Later that year, the English geneticist John Maynard Smith offered his own assessment of the recent contributions of paleontologists to evolutionary theory, which on the whole was quite positive. Beginning by lamenting the relative lack of evolutionary contributions from paleontologists from the 1940s onward, he explained that the tendency among even the more theoretically minded paleontologists had been merely "to show that the facts of palaeontology were consistent with the mechanisms of natural selection and geographical speciation . . . rather than to propose novel mechanisms." In response, "the attitude of population geneticists to any palaeontologist rash enough to offer a contribution to evolutionary theory has been to tell him to go away and find another fossil, and not to bother the grownups."[1] However, over the last ten years, he reports, this attitude has changed, thanks in large part to the work being done by theoretical paleontologists like Gould. His now-famous closing sentence (at least among paleontologists) reads, "the palaeontologists have too long been missing from the high table. Welcome back."[2]

Generally speaking, Maynard Smith's assessment of the contributions of paleontology to evolutionary theory between the formation of the modern evolutionary synthesis and the late 1970s is an accurate reflection of, at the very least, the general view of evolutionary biologists towards their fossil-collecting cousins. One might indeed go back much further, to the very establishment of the theory of evolution by Charles Darwin, to find the source of biologists' uncharitable attitude toward paleontology. Despite the fact that paleontological evidence played a vital role in demonstrating evolutionary succession, in what appears in retrospect to be a profound irony, even as Darwin elevated the significance of the evidentiary contribution of paleontologists, he also had a major hand in condemning paleontology to second-class disciplinary status. One of his greatest anxieties was that the incompleteness of the fossil record would be used to criticize his theory: that the apparent gaps in fossil succession could be cited as, at the very least, negative evidence for the gradual and insensibly graded evolution he proposed. (He also fretted at the complete absence of Precambrian fossils—a topic addressed by more than one of the chapters in this volume). At worst, he worried that the record's imperfections would be used to argue for the kind of spontaneous special creation of organic forms promoted by theologically oriented naturalists whose theories he hoped to obviate. His strategy in the *Origin*, then, was to scrupulously examine every possible vulnerability in his theory, and as a result he spent a great deal of space apologizing for the sorry state of the fossil record.

The metaphor Darwin chose in his apology for the fossil evidence was that of a great series of books from which individual pages had been lost and were likely unrecoverable. "I look at the natural geological record" he continued, "as a history of the world imperfectly kept, and written in a changing dialect; of this history we possess the last volume alone, relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines."[3] Darwin's theory revolutionized paleontology, since the fossil record became the only potential source of evidence that evolution had occurred and for interpreting the history of organic change. Darwin's dilemma, however, was that he both needed paleontology and was embarrassed by it. Even though he celebrated the contributions of paleontologists, he simultaneously undercut any claims their emerging discipline might have for autonomy within evolutionary theory, and this attitude was internalized both by paleontologists and biologists over much of the subsequent history of evolutionary theory.

This view is in evidence as early as the late nineteenth century: in an 1889 review essay in *Nature*, an anonymous author (known only as "E. R. C.") put the attitude of many nonpaleontological observers succinctly: "The palaeontologist has been defined as a variety of naturalist who poses among geologists as one learned in zoology, and among zoologists as one learned in geology, whilst in reality his skill in both sciences is diminutive."[4] Aside from his rather negative opinion of paleontology (he later calls the study of fossils "a definite hobby"), this short essay is significant because it marks the first instance in the literature of the use of the term *neontology* to refer to the study of living organisms. Overall, though, "E. R. C." expressed a view that would become common among biologists, geologists, and even some paleontologists themselves: that subordinating paleontology to geology would provide "a better chance for the cultivation of true geology, which now, to some extent, has its professional positions, its museums, and its publications invaded by these specialists [i.e., by paleontologists]."[5] Clearly, there were more than intellectual issues at stake here. With limited resources available in academic and museum institutions for geology, it was natural for scientists in established departments to want to preserve what they viewed as the traditional core of their disciplines, which for geologists was the study of sediments, minerals, and stratigraphy.

A survey of statements regarding paleontology and its potential contributions by important biologists between 1900 and 1945 reveals the extent to which the discipline had sunk in the eyes of the larger evolutionary community. For example, T. H. Morgan, whose study of the genetics in populations of fruit flies was a landmark in twentieth-century biology, offered the following sneering evaluation of paleontology in 1916:

> Paleontologists have sometimes gone beyond this descriptive phase of the subject and have attempted to formulate the 'causes,' 'laws' and 'principles' that have led to the development of their series. . . . The geneticist says to the paleontologist, since you do not know, and from the nature of your case you can never know, whether your differences are due to one change or to a thousand, you can not with certainty tell us anything about hereditary units which have made the process of evolution possible. And without this knowledge there can be no understanding of the causes of evolution.[6]

A much more widely read echo of this attitude is found in Julian Huxley's *Evolution: The Modern Synthesis* (1942), which served as a kind of manifesto for the synthetic movement. Huxley opined that many paleontologists had been misled toward orthogenesis and Lamarckism because "the paleontologist, confronted with his continuous and long-range trends, is prone to misunderstand the implications of a discontinuous theory of change."[7] Paleontological data is inherently suspect because the fossil record is unreliable: it is incompletely preserved, and the material that *is* preserved is insufficient to inform theoretical conclusions. Or, as Huxley bluntly puts it, "paleontology is of such a nature that its data by themselves cannot throw any light on genetics or selection. . . . All that paleontology can do . . . is to assert that, as regards the type of organisms which it studies, the evolutionary methods suggested by geneticists and evolutionists shall not contradict its data."[8] In other words, paleontologists should be content with the role assigned them ever since Darwin—to document and verify historical confirmation of the processes biologists proposed guided evolution, but not to leap to independent conclusions.

As Maynard Smith's essay notes, even the great George Gaylord Simpson, the American paleontologist who, along with Ernst Mayr and Theodosius Dobzhansky, helped establish the modern synthesis in the 1940s, shied away from demanding complete theoretical equality for paleontologists. One of the broadest and most lasting contributions of his masterpiece, *Tempo and Mode in Evolution* (1944), was its suggestion that paleontology and the fossil record have something unique to say about macroevolution. However, when Simpson sat down to revise *Tempo and Mode* in the early 1950s, a major shift in his thinking appears to have taken place, which led him to significantly downplay his earlier assertion of the theoretical autonomy of paleontology. Exactly why he did this is the subject of some debate, but Gould and others have suggested that Simpson capitulated to pressure from biologists and geneticists to endorse, in Gould's words, "a more rigid selectionism" that favored the selection of small genetic changes—which take place on a scale nearly invisible in the fossil record—as the primary mechanisms of evolution.[9]

From one perspective, it was a legitimate triumph for paleontologists that their discipline was recognized so prominently in the institutionalization of the synthetic theory. Without question, this was largely due to Simpson's efforts, which were, undeniably, heroic. It would be a mistake, however, to conclude that paleontology was, in 1944 or afterward, a fully equal and respected partner in the community of neo-Darwinian evolutionary biology. Paleontologists would certainly benefit from greater participation in the evolutionary biology community—more secure institutional positions, greater respect for their data, better access to mainstream publications and conferences, and a larger stake in theoretical discussions all followed over the next few decades. But there was a cost as well: the synthetic party line discouraged paleontologists from approaching macroevolutionary analysis of the fossil record with confidence that paleontology had unique access to patterns and processes of evolution undetectable by genetics or systematics. Even Maynard Smith proved to be a fickle friend to paleontology: writing in the *New York Review of Books* in 1995, he infamously said of Gould "the evolutionary biologists with whom I have discussed his work tend to see him as a man whose ideas are so confused as to be hardly worth bothering with," adding "he is giving non-biologists a largely false picture of the state of evolutionary theory."[10]

THE PURPOSE OF THIS BOOK

What this book is about is the major transformation in the approach of paleontologists toward questions of a theoretical, evolutionary nature, most of which have taken place over the last forty-odd years, or roughly between 1970 and the present. Given the history of the discipline, it seems all the more remarkable that, as Maynard Smith put it in 1984, "in the last ten years . . . this situation has been changed by the work of a group of paleontologists, of whom Gould has been a leading figure."[11] The 1970s saw a host of exciting new ideas in paleontology, not least of which were areas Maynard Smith himself pointed to in his essay: the theory of punctuated equilibrium, the hierarchical model of selection, species sorting, and mass extinction theory. What Maynard Smith appears to be describing is a bona fide revolution in science—in Thomas Kuhn's terms, the establishment of a new paradigm to overthrow the old, stodgy order. Unknown to Maynard Smith (or at least unremarked), however, was a tradition in paleontology that goes back to at least the 1950s, and features the work of pioneers in the field such as Norman Newell in the United States and Otto Schindewolf in Germany, each of whom practiced a theoretical paleontology, and each of whom trained important figures of the 1970s revolution. Indeed, there are as many elements of continuity as there are of revolution in the history of modern paleontology, and this book will take no official position on the significance, revolutionary or otherwise, of that innovative burst of ideas. Nonetheless it is widely acknowledged that *something* important happened to paleontology in the last few decades, and the chapters that make up this volume will tell versions of that story from a variety of perspectives.

The core of this book are the chapters—more than a dozen in all—written by the paleontologists themselves, all of whom were on hand to experience the exciting events of the 1970s and 1980s first hand. Many of our contributors had major roles in shaping the character of paleontology during this period, and it is the position of the editors that the most valuable contribution of this volume is that it records, in many cases for the first time, these first-hand accounts, recollections, and retrospective evaluations by the scientists who have been most active in the field. Because the contributors have been asked to write for an educated general audience, this book also provides an opportunity for readers who wish to become more intimately acquainted with paleontology's technical contributions to evolutionary theory to learn directly from leaders in those areas of the field. Several historians and philosophers have also been invited to participate, since we hope this volume will also help stimulate interest in further study of the history and conceptual development of modern paleontology.

This book is divided into three sections. Part I, Major Innovations in Paleobiology, examines the growth and development of some of the central ideas in modern paleobiology. A major theme is the relationship between the study of broad patterns of evolution, biodiversity, and extinction, which often rely on statistical examination of large computer databases, and the continued empirical study and collection of fossil data. Most of the chapters in Part I discuss ongoing debates and issues within and surrounding paleobiological research into evolutionary trends and processes, though historical background is often provided to give the reader context to appreciate the significance of current thinking. David Sepkoski begins by providing a historical overview of paleobiology, from the origin of the term itself through the emergence of a distinct set of paleobiological methods and questions in the 1950s and 1960s. He emphasizes that while paleobiology experienced an accelerated period of activity during the 1970s and 1980s, its roots were firmly established by the work of the previous generation of paleontologists, particularly by George Gaylord Simpson and Norman Newell. Next, Michael Benton examines modern approaches to perhaps the oldest problem in paleontology: the perceived incompleteness of the fossil record. Benton examines recent approaches in molecular phylogenetics and statistical tests of paleontological sampling error, concluding that while accurately interpreting the fossil record still presents many challenges, future prospects in paleobiology are quite good. Richard Fortey then turns to the question of the distribution and evolution of marine life in the early Paleozoic, and examines the lessons of recent studies of biogeography and biodiversity for paleobiology. Fortey stresses that both continued study of broad patterns and detailed empirical taxonomic work are necessary to solve problems in biogeography and evolution.

The next chapters in Part I focus on paleobiological studies of specific groups of organisms, and on the lessons the histories of these particular investigations have for paleobiology generally. Richard Aldridge and Derek Briggs' chapter discusses the study and interpretation of the conodonts, a group of extinct animals whose identification and anatomical reconstruction was a mystery and a challenge throughout much of the twentieth century. Their chapter highlights the difficulties posed to paleontologists by fossils whose soft-tissue structure is unclear, and the particular case of the conodonts is presented as a fascinating paleontological detective story in which the authors were major participants. J. William Schopf turns the discussion to the early history of life by describing the solution to one of the great mysteries in the history of science—the absence of Precambrian fossils. Schopf, himself one of the pioneers in Precambrian paleontology, narrates the story of the gradual expansion of the fossil record over the past several decades, including the discovery of microfossils dating some 3.5 billion years old. Next, Jack Horner's contribution examines dinosaur paleobiology, and in particular looks at interpretations of dinosaur evolution. Horner argues that dinosaur paleontologists were among the first to reach the evolutionary high table, and his chapter provides a summary of the many exciting discoveries that he and other researchers have made in recent decades. Tim White's survey of hominid paleobiology rounds out this group of chapters, which describes the history of modern interpretations of human evolution. White examines institutional, intellectual, and popular factors in evolutionary interpretation of hominids, including the influence of larger debates such as cladistics and punctuated equilibrium and the disciplinary identity of paleoanthropology.

The last two chapters in Part I address major theoretical questions in contemporary paleobiology. Patricia Princehouse's provocative essay investigates whether Niles Eldredge and Stephen Jay Gould's theory of punctuated equilibrium challenges the central foundations of Darwinism. Princehouse argues that, ultimately, punctuated equilibrium sparked important work on hierarchy in natural selection that was instrumental in gaining recognition and respect for paleobiology among evolutionary biologists. Finally, Francisco J. Ayala discusses the relationship between evidence for evolution provided by molecular biology and the paleontological evidence in the fossil record. Ayala asks whether molecular data establishes a more reliable evolutionary clock than the fossil record, and his chapter underscores the continued tension between paleontological and biological approaches to evolutionary theory.

Part II, The Historical and Conceptual Significance of Recent Paleontology, moves from a consideration of specific and ongoing problems in current paleobiology to a historical and philosophical examination of themes and issues central to the last forty years of paleobiological thought. The first three chapters of this section discuss primarily philosophical topics: Derek Turner asks whether paleontology, as a historical science, can perform experiments, and whether paleobiological experiments are like experiments in other disciplines. Turner distinguishes between important methodological strategies in empirical testing used by paleobiologists, focusing specifically on the problem of apparent trends in the evolution of body size. Todd Grantham examines the emergence of taxic paleobiology during the early 1980s, which was advocated by its proponents as a solution to the problem of independent levels of selection within the evolutionary process. Despite the prominence of these claims, Grantham argues that taxic paleobiology did not produce consensus between paleontologists and other evolutionary biologists, and may have even widened disagreement between those two groups about fundamental macroevolutionary mechanisms. Finally, David Fastovsky shifts attention to questions about the popular appeal and relevance of paleontology by examining the social and political meaning of dinosaurs in popular culture. Focusing on three case studies, Fastovsky argues that important discoveries about the biology, behavior, and extinction of dinosaurs were influenced not just by empirical developments, but also by the social climate of the times in which they were produced.

The next chapters in Part II address historical foundations of paleobiology outside the United States. Susan Turner and David Oldroyd describe the discovery, by the Australian paleontologist Reginald Sprigg in 1946, of the famous Ediacaran fauna, which included some of the earliest fossils then known. Sprigg's discovery, they argue, helped pave the way for Precambrian paleobiology, and furthermore illustrates the sometimes tortuous path of ideas to scientific acceptance: Sprigg's findings, made by a young and relatively unknown scientist, were not accepted until their later appropriation by Charles Walcott, of Burgess Shale fame. Next, Manfred Laubichler and Karl Niklas examine the important morphological tradition in German paleontology, which in many ways developed its own paleobiology independently of both the Anglo-American tradition and the Modern Evolutionary Synthesis. By investigating the careers of three mid-twentieth-century German scientists—Otto Jaekel, Walter Zimmermann, and Otto Schindewolf—Laubichler and Niklas identify a pluralistic, biologically oriented German paleontology that both predated and anticipated many of the concerns of the paleobiology movement in the United States.

The last four chapters in Part II are historical studies of major theoretical shifts in paleobiological thinking. David Sepkoski investigates the origin and early history of the theory of punctuated equilibrium, from its first articulation in 1971 through subsequent revision and reaction into the early 1980s. Sepkoski addresses the central claim by many observers—that Gould's version of the theory was intended as a challenge to orthodox Darwinism—by examining immediate and later reactions in both published and unpublished sources, and focuses especially on the relationship between Gould and his friend Thomas J. M. Schopf. The subject of John Huss' contribution is another theory in which Gould and Schopf figure prominently: the so-called "MBL" model of simulated clade shape, which was first proposed shortly after punctuated equilibrium was announced. Huss discusses the factors that led the model's authors (who included David M. Raup and Daniel Simberloff, in addition to Gould and Schopf) to propose their idea, and examines both the significance of and objections to the model, concluding that the MBL model offers important lessons about theory testing and simulation that resonate beyond paleobiology. Rounding out a trio of chapters examining the contribution of Gould and his colleagues is Joe Cain's examination of the sometimes testy relationship between members of the new generation in paleobiology and the older guard. Specifically, Cain asks why Gould attacked legendary paleontologist G. G. Simpson, arguing that this "ritual patricide" was central to Gould's efforts at establishing a new disciplinary identity for his favored brand of macroevolutionary paleobiology. Lastly, Arnold Miller presents a historical analysis of the publication and reception of the famous "Consensus Paper" (1981), in which five competing interpretations of global marine diversity were reconciled. Miller uses this paper and the work of its authors (Jack Sepkoski, Richard Bambach, David Raup, and Jim Valentine) as a way of examining disagreements over trends in biodiversity, consensus-building in science, and the shaping of the paleobiological agenda in the early 1980s.

The final section, Part III, offers personal reflections on careers in paleobiology by many of the scientists who shaped the paleobiological revolution. These chapters provide valuable insight into many of the ideas, questions, and themes discussed in the earlier sections, but will also be valuable for scholars and students as an original contribution to the historical record of the growth of modern paleobiology. James W. Valentine, one of the pioneers in the field of paleoecology during the 1960s and 1970s, describes his personal experiences as a scientist committed to integrating paleontological and biological study. In particular, Valentine discusses early attempts to relate faunal associations and fossil distributions, and also the current and future significance of molecular biology for paleontology. Richard Bambach, another leader in the establishment of paleobiology during the early 1970s, presents his personal journey as a paleoecologist and evolutionary paleobiologist from the 1950s through the 1990s. Bambach's account sheds light on the important connections between paleoecology and paleobiology, and his personal experiences track many of the central developments of the paleobiological revolution. Rebecca German offers the fascinating insights of someone who was a student of paleobiology during the 1970s, and her personal account of mentors such as David Raup, Tom Schopf, and Stephen Jay Gould sheds important light on the role of pedagogy during the paleobiological revolution. German describes how formal and informal instruction shaped the next generation of paleobiologists, and provides a glimpse of the field not normally accessible through published research.

Breaking with the largely American perspective of the other personal accounts, Anthony Hallam offers the perspective of a paleobiologist trained in the United Kingdom, and describes the development of paleobiological interests among British paleontologists from the 1950s to the 1980s. Hallam focuses particularly on punctuated equilibrium and the associated theory of species selection, which played an important role in his own research, concluding with an assessment of the significance of the idea of punctuational speciation for paleobiology generally. The next chapter, by Arthur Boucot, also examines punctuated equilibrium, which he compares to the idea of community evolution that emerged from ecological study of the fossil record. A longtime critic of punctuated equilibrium, Boucot identifies what he considers several weaknesses in that theory, and argues that community evolution is based on a more reliable empirical foundation. The personal reflections conclude with the transcript of an interview with David M. Raup, one of the most important theoretical paleontologists of his generation and a major architect of the paleobiological revolution. In this interview Raup discusses his involvement in major debates over macroevolution and extinction throughout the 1970s and 1980s, and also discusses his pioneering work in computer-based simulation and analysis of fossil data.

The final two chapters in this volume offer a general assessment of both the past and future of paleobiology. David Jablonski, one of the leaders of the current generation of paleobiologists, presents his view of the current state of the discipline, and identifies six major areas for investigation that will define paleobiology's future. Jablonski argues for the necessity of continued efforts to unite paleobiology with the wider community of evolutionary biology, and provides an important manifesto for students and practitioners of paleobiology. In the conclusion to the volume, Michael Ruse explicitly addresses the title of this book, asking whether the development of paleobiology over the past several decades constitutes a genuine scientific revolution. Using philosopher of science Thomas Kuhn's definition as a starting point, Ruse evaluates a number of criteria by which this era of paleobiology might be judged to have been revolutionary, and compares the emergence of paleobiology with other major transformations in the modern natural sciences. His conclusion, which would likely be endorsed by all contributors to this book, is that whatever label one uses to describe the growth of paleobiology, it was an event of significant importance in the history of recent science and a subject worthy of continued and serious historical and philosophical study.

NOTES

1. John Maynard Smith, "Palaeontology at the High Table," 401.

2. Ibid., 402.

3. Charles Darwin, *On the Origin of Species*, 310–11.

4. "E. R. C.", "Review of Die Stamme Des Thierreiches, by Von M. Neumayer," 364.

5. Ibid.

6. Thomas Hunt Morgan, *A Critique of the Theory of Evolution*, 25–27.

7. Julian Huxley, *Evolution, the Modern Synthesis*, 31.

8. Ibid., 38.

9. Stephen Jay Gould, "G. G. Simpson, Paleontology, and the Modern Synthesis," in *The Evolutionary Synthesis; Perspectives on the Unification of Biology*, 161.

10. John Maynard Smith, "Genes, Memes, & Minds," *New York Review of Books* 42, no. 19 (1995).

11. Maynard Smith, 1984, 401.

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CHAPTER ONE

The Emergence of Paleobiology

David Sepkoski

In a sense, paleobiology has been around since the beginning of the modern discipline of paleontology. If it is defined simply as the "study of the biology of extinct organisms," as it is in the *Dictionary of Ecology, Evolution and Systematics*, then paleobiology describes what many, if not most, paleontologists have done since at least the early nineteenth century.[1] After all, paleontology is usually defined as the study of fossils—and what are fossils, other than the physical remains of past life? But this simple equation hardly captures what was distinctive, exciting, or different about the research that was promoted over the past forty years by members of the paleobiological movement, which has radically changed the profession of paleontology. The nature of that change—which, broadly, involved theoretical, quantitative reinterpretations of patterns of evolution and extinction—is documented in the chapters that follow, many of which are written by the scientists themselves, who were actively involved in effecting this transformation. This introductory essay puts these fairly recent developments in broader historical context and attempts to identify some of the defining features of paleobiology.

In the modern, disciplinary sense, paleobiologists address their research toward biological questions about fossils and the fossil record, as opposed to investigating geological questions such as the deposit of fossils and their stratigraphic sequence. In practice, this means particularly a focus on the evolution, adaptation, ecology, function, and behavior of extinct organisms. Paleobiologists study both vertebrate and invertebrate fossils, but since the middle of the twentieth century, a major focus has been on invertebrates, which are more richly documented in the fossil record by some orders of magnitude than vertebrate remains. An important reason for this orientation has to do with the methodology of modern paleobiology: since the computer revolution of the 1960s and 1970s, methods of quantitative modeling, analysis, and tabulation have been at the center of the paleobiological approach. The great number of invertebrate fossils collected over the past century has provided an extensive resource for paleobiologists especially interested in studying the large-scale patterns and processes in the history of life, and sophisticated statistical tools developed over the past several decades have made quantitative, computer-assisted research an essential component of paleobiology.

Another, related characteristic of recent paleobiology has been its closer professional relationship with biology and its greater integration into the mainstream of evolutionary studies than was the case fifty years ago. The great American vertebrate paleontologist George Gaylord Simpson was a major architect of the Modern Evolutionary Synthesis during the 1940s and 1950s, but his adamant belief that paleontology and biology are sister disciplines was not widely shared by colleagues in either discipline. One hallmark of paleobiology since that time has been a much greater integration of the study of biology into pedagogy and practice and a concerted effort to both borrow from biological disciplines (especially from genetics and ecology), as well as to bring the fruits of paleontological research to a wider biological audience. This has, of necessity, prompted institutional reorganization among paleontologists—not always an uncontested or uncontroversial endeavor—that has even resulted in the establishment, in a few cases, of autonomous departments or programs in paleobiology at universities and museums. One of the most significant developments on this front was the establishment, in 1975, of the journal *Paleobiology*, which has ever since been the leading outlet for specifically paleobiological research and a major tool for the establishment and promotion of the paleobiological agenda.[2]

That said, there is no single definition that would be agreed upon by all paleobiologists, and even among the various authors in this volume there is substantial difference of opinion about what the central methods and assumptions of paleobiology should be. This essay, then, takes a historical approach to understanding the character of paleobiology—from the emergence of the term to the fairly recent past—and will let paleontologists speak for themselves in the following chapters about its current meanings. One conclusion that all observers would agree on, though, is that the discipline has changed remarkably over the past several decades; this essay locates the roots of that change even further back, to the beginning of the twentieth century, and examines some of the themes and debates that have characterized paleobiology's emergence from the shadow of geology and biology.

PALEONTOLOGY AFTER DARWIN

When Charles Darwin was developing his theory of evolution, biology and paleontology had not yet become firmly established as independent disciplines, and as a naturalist, Darwin simply marshaled and interpreted the available evidence from all fields as they best supported his argument. These arguments drew freely on paleontology, biology, geology, and related subjects, and it would be fair to say that *Origin of Species* presented evidence from the fossil record that might be considered paleobiological. But the aftermath of the publication of *Origin* was a period that saw significant disciplinary reorganizations, and one result was that scientists became increasingly aware of distinct disciplinary identities. A number of historians have written about the emergence of the experimental tradition in biology during the second half of the nineteenth century, which contributed greatly to the trajectory evolutionary study took after 1859.[3] In mimicking some of the laboratory practices and methods of established disciplines like physics and chemistry, biologists greatly enhanced the prestige and autonomy of their field. The emphasis in post-*Origin* biology was on uncovering the mechanisms of heredity, which, although not fully accomplished until the turn of the twentieth century and the rediscovery of Gregor Mendel's work, nonetheless made great strides in identifying cell structures responsible for heredity (e.g., chromosomes) and studying the physiological processes of biological development (such as patterns in ontogeny).[4]

This turn toward biology as the central evolutionary discipline indirectly contributed to the formation of a disciplinary identity for paleontology. Darwin had stated, more or less, that paleontology had already provided everything it was likely to contribute to understanding evolution, so for supporters of Darwin there was no great urgency to scrutinize the fossil record. In fact, Darwin's supporters were more likely to want to push paleontology into the background: as William Coleman argues, "to the biologist that [fossil] record posed more problems than it resolved . . . the incompleteness of the recovered fossil record, in which a relatively full historical record for any major group was still lacking, was the very curse of the transmutationist."[5] As a result, there were really only three alternatives available to paleontologists with regard to evolutionary theory: (1) to ignore any special theoretical relevance of paleontological data and focus purely on descriptive studies of morphology and stratigraphy; (2) to accept the Darwinian line, but to nonetheless try to improve the quality of the record of isolated fossil lineages to support Darwin's theory; or (3) to reject Darwinian evolution and seek some other theoretical explanation of evolution in which fossil evidence could be brought more directly to bear.

Over the next hundred years (and perhaps even longer), the majority of working paleontologists tended toward a position that was essentially agnostic toward evolutionary theory. This did not mean rejecting Darwin or evolution—it simply meant their *work* did not attempt to make any comment or contribution to the theory. In the early twentieth century this attitude became even more prevalent, as the burgeoning petroleum industry's demand for paleontological expertise swelled the ranks of paleontologists with scientists whose interest in the field was economic.[6] Those nineteenth- and early twentieth-century paleontologists who did pursue larger interpretive questions about the fossil record tended to subscribe to non-Darwinian, directional evolutionary models like Lamarckism and orthogenesis, which had the effect of further marginalizing paleontology from biology.[7]

By the early twentieth century, paleontology was fairly isolated from biology and other evolutionary disciplines: the most spectacular advances in the field had been in the collection of large vertebrate fossils, and broad, empirical studies of evolutionary pattern and process were not actively pursued. Rightly or wrongly it was also perceived that paleontologists had abandoned Darwinism and natural selection, which alienated those evolutionary biologists who were still committed to Darwinian orthodoxy, and for which paleontology would pay heavily when Darwinism emerged triumphant in the mid-twentieth century. Finally, from an institutional perspective, paleontology was in danger of losing all contact with biology: isolated in geology and museum collections departments, paleontologists had little regular interaction with experimental biologists. This led to mutual mistrust and incomprehension between the two fields, which was only exacerbated after the genetic turn in biology following the rediscovery of Mendel. Darwin may have considered paleontology, geology, and biology to be equal partners in the enterprise of evolutionary natural history, but as the twentieth century began, they were separated by a fairly wide gulf.

Nor, as it turned out, was the methodology adopted in the nineteenth century by most vertebrate paleontologists adequate to meet the demands of biologists' emerging conception of rigorous quantitative science: vertebrate paleontology was descriptive first and foremost, and quantitative paleontological analysis was limited to the most cursory kinds of anatomical measurements and tabulations. Biology, on the other hand, underwent a quantitative revolution in the first several decades of the twentieth century, where "the attachment of numbers to 'nature'—and the growing measurability and testability of natural selection within a populational framework" helped produce "a mechanistic and materialistic science of evolution that could rival Newtonian physics."[8] The impetus for this transformation was the discovery of quantitative laws of heredity, such as the Hardy-Weinberg principle of stable genetic equilibrium, which established a mathematical basis for confirming the expectations of natural selection in populations.[9] Paleontologists simply had no way of translating their data into terms that population biologists and geneticists could make use of, and, until G. G. Simpson stepped to the fore in the 1940s, remained mostly invisible to evolutionary biologists.

Despite paleontology's rather lowly status among biologists, it was in fact during the early decades of the twentieth century that the term *paleobiology* first began to be used. The earliest record of the word comes from an 1893 paper in the *Quarterly Journal of the Geological Society of London*, by S. S. Buckman, who commented on the usefulness of a term that "I may call 'palæobiology.'"[10] However, the much more likely source for the eventual widespread usage of the word is the Austrian vertebrate paleontologist Othenio Abel, who began using the term *päleobiologie* to describe biologically informed paleontology as early as 1912. In that year, he published *Grundzüge der Paläobiologie der Wirbeltiere* (*Fundamentals of Vertebrate Paleobiology*), followed by *Paläobiologie der Cephalopoden* in 1916; his most widely read work among English-speaking paleontologists was *Paläobiologie und Stammesgeschichte* (*Paleobiology and Phylogeny*), published (but never translated) in 1929. Abel was a distinguished professor of paleontology at the universities of Vienna and Göttingen, where he had a significant influence on German paleontology before the war, and in Vienna was also responsible for founding the journal *Palaeobiologica* in 1928 as the official organ of the Viennese *Paläeobiologischen Gesellschaft*.[11]

Abel is an interesting case. Theoretically, he was sympathetic to the idealist tradition of directional evolution, and supported a version of orthogenesis, but as Peter Bowler notes, he "made at least a pretense of conforming to a mechanistic language" in describing his theory.[12] For example, in *Paläobiologie und Stammesgeschichte* Abel wrote "we need assume neither a supernatural principle of perfection, nor a principle of progression, nor a vital principle"; nonetheless "the phenomenon of orthogenesis, which has often been disputed but now can no longer be denied, is transmitted by the mechanical law of inertia into the organic world."[13] However, he was also a strong proponent of the biological basis for paleontological theory, and his orthogenetic beliefs were not cultured in isolation from biology (as were the views of many American paleontologists, including Cope and Osborn), nor did he reject all of the adaptationist tenets of Darwinism. In fact, he argued that "research on adaptation had originally cultured the nucleus of paleobiology" in Darwin's day,[14] and he lamented the subsequent exclusion of paleontology from biology:

> One should think that through the appearance of this work [*Origin of Species*], which produced such an enormous revolution in biology, paleontological research would all at once be steered onto a new path, and that the basis for these sorts of [paleobiological] investigations were prepared here. It is so much the more astounding that paleontology held itself in the background for so long, and can scarcely take its place in that eternally lively discussion, in any case not to the extent as the depth of the available knowledge of fossils allowed at that time.[15]

In other words, Abel argued that paleontology had been prevented from taking its place at the evolutionary high table in part by its subordination to geology, a complaint that would become more and more common among paleontologists over the next several decades. Abel concluded, however, that paleobiology had a decisive role to play in evolutionary theory: "Among all phylogenetic research disciplines paleobiology stands alone in being able to demonstrate historical documentation, and to make readable and to draw conclusions from these facts."[16]

Abel's work was read reasonably widely by American paleontologists, and he is cited repeatedly in Simpson's groundbreaking *Tempo and Mode in Evolution* (1944). Simpson did not approve of Abel's reliance on orthogenesis to explain the evolution of horses (at one point calling Abel's belief "naïve"), but it is certain that Abel's general message about the ambitions of paleontology were received more warmly.[17] For example, in 1926 Simpson published a paper on the evolution of Mesozoic mammals, which he described as "a study in paleobiology, an attempt to consider a very ancient and long extinct group of mammals not as bits of broken bone but as flesh and blood beings."[18] This was Simpson's first use of the term *paleobiology*, and the paper prominently cites Abel's *Grundzüge der Paläobiologie der Wirbeltiere*. He also recalled many years later that "while still in graduate school I found Othenio Abel's books particularly interesting and useful."[19] Simpson was a committed reader of German scientific literature (he later reviewed German paleontological publications in the journal *Evolution* for his linguistically challenged colleagues), and at the very least his (and others') familiarity with Abel's work probably accounts for the origin of the term *paleobiology* in its modern context.[20]

Nonetheless, paleontologists in the first several decades of the twentieth century generally reflected the attitudes projected onto their discipline by biologists. Ronald Rainger concludes that despite the biological interests of people like Abel, "interest in such biological questions did not transform the discipline of paleontology. In the 1920s, just as in the 1880s, many students of the fossil record remained preoccupied with descriptive, taxonomic questions, and vertebrate paleontology was still primarily a museum science."[21] According to Rainger, this state of affairs persisted until Simpson offered his radical reevaluation of paleontological goals and methods. This assessment is probably accurate for the bulk of paleontological practice in the first part of the twentieth century, but it is important not to diminish the continuity between Simpson and his predecessors, or to overstate the discontinuity between Simpson's approach and prior paleontological theory. Paleontologists up to and during the synthesis elaborated a theoretical agenda for their discipline, and Simpson's voice was perhaps just the loudest and most persuasive among many of his contemporaries'.

PALEONTOLOGY AND THE MODERN EVOLUTIONARY SYNTHESIS

The "Modern Synthesis" of evolutionary biology has been fairly consistently defined by historians as the sum total of theoretical development, roughly between 1937 and 1950, whereby the genetic principles of Mendelian heredity were accommodated to Darwin's theory of natural selection.[22] In other words, biologists applied the knowledge of heredity accumulated by geneticists in the first decades of the twentieth century to the principles of gene flow as determined by ecologists and biologists studying adaptation and selection in populations. The resulting synthesis defined evolutionary biology as a study of the movement (via inheritance and mutation) of *genes* within *populations*. One of the most important aspects of the synthetic approach was the development of a quantitative understanding of gene flow in populations, which allowed biologists to confirm that Darwin's qualitative assessment of the sufficiency of natural selection to produce evolution agreed with the modern understanding of genetics.[23] The doctrine produced by the end of the synthesis period became commonly known as "neo-Darwinism."

G. G. Simpson, who came into close collaboration with biological colleagues like Ernst Mayr and Theodosius Dobzhansky at Columbia University and the American Museum of Natural History, was a major figure in establishing the Modern Synthesis, and he undeniably brought new attention and respectability to paleontology within evolutionary biology. It would be a mistake, however, to conclude that paleontology was, in the 1940s or afterward, a fully equal and respected partner in the neo-Darwinian community. Paleontologists would certainly benefit from greater participation in the evolutionary biology community—more secure institutional positions, greater respect for their data, better access to mainstream publications and conferences, and a larger stake in theoretical discussions all followed over the next few decades. But there was a cost as well: as Patricia Princehouse argues, "in large part the modern synthesis served to sideline major research traditions in paleontology."[24] One of those traditions involved approaching macroevolutionary analysis of the fossil record with confidence that paleontology had unique access to patterns and processes of evolution undetectable by genetics or systematics.

Simpson's role in this aspect of the story is complex. He was perhaps the most influential paleontologist of the twentieth century, and his masterpiece, *Tempo and Mode*, has been read by generations of paleontologists and biologists. He was also, however, in many respects an iconoclast, and even as he appealed to the biological understanding of evolution promoted by the other major architects of the synthesis, his vision was significantly at odds with many of his paleontologist colleagues. Simpson appears to have been aware of how radical his views were—both for biologists *and* paleontologists. Echoing the sentiments of many contemporary biologists, he later recalled that "at the time when I began to consider this subject [of evolution] I believe that the majority of paleontologists were opposed to Darwinism and neo-Darwinism, and most were still opposed in the early years of the synthetic theory."[25]

Even before publishing *Tempo and Mode*, Simpson had already announced his intention to revitalize paleontology by increasing the discipline's analytical rigor. With his wife, the psychologist Anne Roe, Simpson began preparing a book on biological statistics in the mid-1930s. The product of this collaboration was a textbook titled *Quantitative Zoology* (1939), which was a primer in mathematical and statistical analysis for zoologists and paleontologists. In the preface, Simpson and Roe note that while it is "proper" for zoologists to avoid relying on an a priori mathematical framework, nonetheless the behaviors and characteristics of actual organisms can be profitably translated into a symbolic language.[26] The central problem the authors hoped to address was that "whether from inertia, from ignorance, or from natural mistrust . . . most zoologists and paleontologists distrusted the overt use of any but the very simplest and most obvious numerical methods."[27]

Simpson began writing *Tempo and Mode* while he and Roe were still finishing *Quantitative Zoology*, but publication was delayed until 1944, after Simpson returned to the United States from active military duty. In the preface, he notes that "the final revision was made under conditions of stress," and that because of the circumstances several "important studies" relevant to his subject were omitted.[28] Simpson is obliquely referring here to Huxley's *Evolution: The Modern Synthesis* and Mayr's *Systematics and the Origin of Species*, both of which were published in 1942, after he had begun his service. He had, however, read Dobzhansky's *Genetics and the Origin of Species*, and that work had a profound influence on his vision of evolutionary paleontology. In later years, Simpson stressed the importance of this encounter: "The book profoundly changed my whole outlook and started me thinking more definitively along the lines of an explanatory (causal) synthesis and less exclusively along lines more nearly traditional in paleontology."[29] It also "opened a whole new vista to me of really explaining the things that one could see going on in the fossil record and also by study of recent animals," and allowed him to relate his own paleontological research to the exciting new work in genetics.[30]

Probably the single most important influence Dobzhansky had on Simpson was to push the latter to think about the history of life (and the evidence of the fossil record) in terms of the genetics of once-living populations. The major argument of *Tempo and Mode* is that what happens on the Darwinian population level explains transformations in the fossil record, and that those transformations can be explained using models of population genetics. Paleontology, Simpson stressed, could be useful for uncovering the mechanisms that drive evolution, and not just for documenting the physical historical record. As he wrote in the introduction, "like the geneticist, the paleontologist is learning to think in terms of populations rather than of individuals and is beginning to work on the meaning of changes in populations."[31] Simpson's great insight was that paleontology could be modeled after population biology with the additional dimension of *time*—he described *Tempo and Mode* as a work in "four-dimensional" biology, where the distribution and transformation of organisms could be tracked in a temporal geography analogous to physical geography. He emphasized that the temporal (or historical) element of paleontology offered a unique and critical perspective to evolutionary theory, and the importance of this message cannot be overstated: after *Tempo and Mode*, temporal biogeography became central to paleontological evolutionary theory.

One of *Tempo and Mode*'s broadest and most lasting contributions to evolutionary theory was its suggestion that paleontology and the fossil record have something unique to say about macroevolution. The synthetic view of macroevolution—endorsed by Dobzhansky, Mayr, Huxley, and many others—held that major evolutionary patterns at the higher taxonomic levels are simply extrapolated effects of microevolution. As a paleontologist, however, Simpson had a keener eye for the apparent discontinuities in the fossil record than his colleagues Mayr and Dobzhansky, and his approach to macroevolution reflected this. In *Tempo and Mode* he argued that the ubiquity of extrapolation from microevolution was not a settled matter. Simpson's theory broke evolution into three tiers: the first, microevolution, basically followed the Synthetic account. Macroevolution, the second tier, accounted for broader patterns, but it was a third process, "mega-evolution," which brought about major taxonomic changes. In order to account for the seemingly abrupt transitions in the fossil record, Simpson introduced the idea of *quantum evolution*, which described accelerated evolutionary change among small populations that due to geographic isolation had come into disequilibrium.[32] Simpson suggested that quantum evolution probably utilized basic microevolutionary mechanisms of random mutation and natural selection (and not saltations), but he emphasized that such accelerated change might constitute an independent process. While his theory was not necessarily opposed to the broader Synthetic view, it certainly raised eyebrows with the provocative statement that "if the two [macro- and microevolution] 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."[33]

It is sufficient to note here that, while not explicitly in conflict with the synthetic theory of evolution, Simpson's approach to macroevolution and the fossil record was somewhat idiosyncratic. Stephen Jay Gould notes that while Simpson's approach to the fossil record was "consistent with genetic models devised by neontologists" in that it held "adaptation as the primary cause and result of evolutionary change," and maintained that "continuous transformation of populations" explains directional patterns in evolutionary history, nonetheless Simpson left the door open for other explanations.[34] In particular, he argued that sequential discontinuities in the fossil record (especially across taxonomic categories) might not always be artifacts of imperfect preservation: "the development of discontinuities between species and genera, and sometimes between still higher categories, so regularly follows one sort of pattern that it is only reasonable to infer that this is normal and that sequences missing from the record would tend to follow much the same pattern."[35] In fact, Simpson continued, "the face of the fossil record really does suggest normal discontinuity at all levels," an observation whose significance for evolutionary theory is unclear.[36] While he notes that many observed gaps in the fossil record are likely "a taxonomic artifact," this does not adequately explain the systematic occurrence of the gaps between larger units.[37]

A final, important feature of *Tempo and Mode* is its commitment to a quantitative, analytical method. As suggested earlier, many biologists and even some paleontologists had dismissed all hope of paleontology ever reaching the quantitative sophistication of most other scientific disciplines, including biology. This pessimism contributed greatly to paleontology's theoretical subordination as a discipline, and quite likely even discouraged many bright, analytical students from pursuing the profession. Simpson, however, was determined to apply the methodology he promoted in *Quantitative Zoology* to paleontological data, and in this regard his effort was genuinely revolutionary. Gould calls Simpson's "use of quantitative information . . . [his] second greatest departure from traditional paleontological practices," which he characterizes as "a novel style . . . [of] drawing models (often by analogy) from demography and population genetics and applying them to large-scale patterns of diversity in the history of life."[38]

Perhaps Simpson's most significant use of quantification is his treatment of taxonomic survivorship, or the measure of the longevity of a particular taxon or group. Simpson's approach was to gather taxonomic data from fossil catalogues like K. A. von Zittel's *Grundzüge der Palaeontologie*, from paleontological monographs, or from other systematics literature, and then to tabulate the longevity of the group based on first and last appearances in the record. Next, following the method Raymond Pearl established for statistical demography, he plotted curves representing survivorship over time as a percentage of the initial population.[39] By modifying this data with a number of straightforward statistical devices, Simpson was able to draw out several very interesting conclusions: general patterns of survivorship appear, on the whole, to follow the same, diminishing parabolic curves, although different groups (he compares pelecypod mollusks to carnivorous placental mammals) have widely differing rates.[40] These curves can also be correlated with extant fauna, comparisons can be made within groups over different periods of time, and generalizations about major fauna can be made, all of which, Simpson noted, can shed important light on evolutionary patterns. In succeeding chapters, we will again and again confront examples of "Simpsonian" analytical techniques applied to paleobiology; Simpson's presentation of paleontology's amenability to theoretical modeling and statistical techniques had the greatest possible influence on later generations of paleontologists.

All in all, Simpson's work substantially helped to bring paleontology in line with mainstream attitudes in biology and genetics, and also worked to carve out an independent place within evolutionary biology. As such, Simpson made a major contribution to the early stages of the development of paleobiology. What was necessary following the publication of *Tempo and Mode* (and its successor, *Major Features of Evolution*, a completely revised version, published in 1953) was an active community of paleontologists dedicated to pursuing paleobiological questions. Simpson helped provide the motivation, but others would need to take up the challenge he posed.

THE DEVELOPMENT OF PALEOBIOLOGY

During the 1950s and 1960s a major transformation was quietly taking place in paleontological approaches to evolutionary theory and the fossil record, one which Simpson certainly played a role in starting. This shift involved several distinct but related aspects: first, paleontologists began to actively assess the institutional status of their discipline—asking whether it belonged, for example, with geology, with biology, or rather constituted an independent discipline on its own. Second, paleontologists began more and more to explicitly connect their work with the agenda of the Modern Synthesis, and to publish in outlets (such as the journal *Evolution*) that were read by biologists and geneticists. Even papers in paleontology-specific publications like *Journal of Paleontology* took on a more theoretical cast during this period. Third, and perhaps most significantly, paleontology became quantitative. This is not to say that quantitative methods (measurements and statistical analysis) had been absent from the work of paleontology in the past, but the period between 1950 and 1969 saw a burgeoning interest in addressing broad, synthetic questions about the fossil record (e.g., biodiversity, evolution, extinction) with quantitative rigor and sophistication not previously seen in paleontological literature.

Between 1940 and the later 1960s, a number of paleontologists began to publicly question paleontology's longtime association with geology, and to argue that paleontology—as the study of ancient *life*—belonged more properly among the biological disciplines. For example, in his 1946 presidential address to the Paleontological Society, J. Brookes Knight made a forceful call to arms for paleontologists to throw off the restrictive shackles chaining them institutionally to geology departments. "Because paleontology is not truly a branch of geology," he wrote, "it does not best serve geology when cultivated and applied by geologists," concluding that "because paleontology is the study of the life of the past it is a biological science."[41] These comments touched off a minor controversy in the paleontological community. The first to respond was J. Marvin Weller of the Walker Museum at the University of Chicago, who rejected Knight's call entirely. Arguing that paleontological stratigraphy is "the heart of geology" and its "single great unifying agency," Weller urged paleontologists to stick close to their geological roots.[42] "Invertebrate paleontology is much more closely related to geology than biology" he reasoned, and the two fields are mutually interdependent, whereas biology and paleontology can each "get along" without the other. He had little time for vertebrate paleontologists, whom he considered hardly even geologists, and even less interest in the kind of paleontological-biological synergy preached by his many of his peers: "any student of fossils who does not have a strong, abiding, and well-founded interest in geology . . . is not a paleontologist. He is simply a paleobiologist."[43]

It is especially interesting that Weller used the term *paleobiologist* as an epithet rather than a compliment. However, there were other paleontologists at the time who regarded paleobiology as an approach to be actively pursued, rather than avoided, and none had a greater influence than the invertebrate specialist Norman Newell. It may fairly be argued that nobody did more to promote the agenda of paleobiology in the 1950s and 1960s than Newell, and his influence, measured directly through his work, and indirectly through his mentoring of students and younger paleontologists, was profound. Newell's hand touched nearly every major aspect of paleobiology during his career, and he can be said to have been directly responsible for, in no particular order, the investigation of broad patterns in the fossil record, the development of quantitative approaches to fossil databases, the study of the evolutionary significance of mass extinctions, and the creation of the subdiscipline of paleoecology. Throughout his career, Newell also tirelessly promoted the institutional agenda of paleobiology, and he trained many of the leaders of the movement's next generations.

According to Gould, a student of Newell's who would become one of the most active of that later generation of paleobiologists,

> When virtually all paleontologists were trained as geologists and had no biological knowledge beyond the basics of invertebrate morphology, Norman Newell saw, virtually alone, that the most exciting future direction in paleontology lay in its relationship to evolutionary theory and to

> biological thought in general. I think that only a few very old-fashioned paleontologists would deny today that this prediction, has been fulfilled and that American invertebrate paleontology is now in its most exciting phase since the era immediately following Darwin's *Origin of Species*. With his early monographs, and his persistent encouragement of biological thinking, Norman Newell was the godfather of this movement.[44]

This is strong praise indeed, but leaving aside Gould's somewhat hyperbolic assessment of the status of paleobiology, it is probably an accurate characterization of Newell's contributions. Preston Cloud, with whom Newell pioneered the study of important fossil beds of the Permian of Texas and elsewhere, has remarked that "by his imaginative researches, Newell has been instrumental in a rejuvenation of biological invertebrate paleontology. One of America's foremost invertebrate paleontologists, he is outstanding for his interpretation of fossil invertebrates in the light of the ecology and life histories of living species."[45] And Ernst Mayr agrees, reflecting that "Norman has served as an important bridge between specialized paleontology and evolutionary biology as a whole . . . [and was] quite instrumental in introducing the evolutionary synthesis into invertebrate paleontology."[46]

An example of Newell's vision for paleontology can be seen in an essay that he and Columbia University colleague Edwin Colbert coauthored in response to Marvin Weller's criticism of paleobiology. While the authors noted that "it is not likely that many universities could be persuaded to erect separate paleontology departments," they respectfully offered that "Professor Weller's point of view admirably expresses the traditional (and 'narrow') attitude of the geologist toward paleontology," which "is being modified only too gradually." Paleontology is only considered a branch of geology, Newell and Colbert reasoned, "because paleontologists, through lack of adequate training in biology, have made it so."[47] They proposed a division of paleontology into two categories—stratigraphic and "paleobiology"—and emphasized that even this dichotomy obscured significant areas of overlap between the two approaches. Many of the goals of paleontology transcend stratigraphy, they stressed, such as phylogeny reconstruction and the restoration of the fossil record, but are also beyond the ken of biologists who lack paleontological training. And turning the tables on Weller, Newell and Colbert argued that it is its close traditional association with geology that has, "as much as anything . . . [caused] the lack of mature growth of this branch of [invertebrate] paleontology." In their conclusion, Newell and Colbert centered the issue on paleontology's engagement with evolution: "the invertebrate paleontologist in North America has suffered because of his lack of an *evolutionary* viewpoint, the result of a lack of training in biology."[48]

In addition to pursuing his agenda publicly in *Journal of Paleontology*, Newell also worked to change the mentality at his home institution. In 1948 or 1949, Newell sent a memo to his colleagues in the geology department at Columbia titled "Instruction in Paleobiology," which he described in a handwritten note to Simpson as "part of an unavoidable campaign of missionary work." In it, he outlined his programmatic agenda for revising the way paleontology was taught, and ultimately practiced. "The period between the two world wars," he wrote,

> was characterized by development in invertebrate paleontology chiefly along utilitarian lines, seemingly at the expense of fundamental progress in the science. . . . Because of the traditional union between invertebrate paleontology and geology it has come to be forgotten that the roots of paleontology are in biology, just as geophysics rests on physics. It is a tragedy that paleontology has at last become a 'handmaiden to geology.' Yet the techniques and mass of data of paleontology are now so distinct from geology and biology that the majority of biologists and geologists do not even know what constitutes urgent problems in paleontology. Although it is seldom accorded the status of a separate science, paleontology is just that.

Newell drew particular attention to the problems in the current pedagogical climate: with "the majority of teachers of paleontology" being "stratigraphers or petroleum geologists, concerned entirely with the application of paleontology to geology. . . . Little progress is being made toward an understanding and interpretation of fossils and their life environment." However, Newell saw an opportunity to change this at Columbia, drawing on the rich resources at the American Museum of Natural History (AMNH), to develop "a program of instruction in invertebrate paleontology, or paleobiology, at a professional level, adequate for the development of research specialists."[49]

Newell also promoted paleobiology through the example of his research, which, from the 1950s forward, became more and more concerned with answering broad questions about evolution and extinction using quantitative analysis of the invertebrate fossil record. In a 1959 symposium sponsored by the Paleontological Society celebrating "Fifty Years of Paleontology," Newell gave an overview of the growth of paleobiology that expresses important elements of his agenda for the field. He begins by noting that "from the very beginnings of our science there have been two schools, those who study fossils in order to understand stratigraphy, and those who study fossils in order to learn about past life," and he applauds others who have called for greater biological orientation in paleontology.[50] Newell was pleased to report that "the fossil record is much richer than we formerly supposed," but cautioned that paleontology needed to produce more biologically sensitive workers to meet the demands of the changing profession. He also cited five "truly revolutionary developments of the past three decades": (1) improved collection and preparation of fossils; (2) "recognition of the special importance of populations in taxonomy and evolution"; (3) more attention to ecological context; (4) "the application of statistical methods . . . [to] all sorts of paleontological problems"; and (5) greater understanding of the geochemistry of fossils.[51] Newell contrasted the "gradual increase in appreciation of the positive merits of the fossil record" with Darwin's earlier "preoccupation with the deficiencies in the record," and while he noted a continued "lively debate" over interpretations of the record, he cited a "general agreement . . . that many striking patterns of fossil distributions have been confirmed hundreds of times."[52] In terms of the sheer quantity of paleontological data, Newell pointed to the dramatic improvement of knowledge of the record: whereas Charles Schuchert estimated, in 1910, some 100,000 extant fossil species, Curt Teichert's calculation in 1956 raised that number to ten million.[53] Overall, Newell predicted "the future prospects for paleontology are, indeed, very bright."[54]

Two of Newell's most important contributions to the growth of paleobiology were his study of trends in the sequential succession of invertebrate evolution and his analysis of the role of mass extinction in the history of life. In the first instance, Newell drew attention to the unique set of problems paleontology faces in applying taxonomic divisions to fossil populations. Here his major concern is preservational bias: while "the fossil record is in fact astonishingly rich and meaningful," the 'time dimension' in paleontology complicates matters, since "the selection of species limits in a vertical series might be arbitrary."[55] In other words, the added dimension of time is both a boon and a hindrance to paleontology: within a given horizontal sample (i.e., a group of organisms taken from the exact same stratum or moment in geological time) it might certainly be possible to distinguish taxa, including species and perhaps even subspecies or varieties. But paleontology also has a vertical dimension, and as the taxa identified from horizontal samples continue forward in time it is extremely difficult to discern where taxonomic limits or divisions should be placed. This situation is further complicated by the fact that vertical sequences are almost always interrupted, and the paleontologist is not guaranteed to fill in these gaps by further collection. Finally, as Newell notes, horizontal and vertical perspectives must be combined to get an accurate picture of the influence of geography on phyletic evolution.[56] Nonetheless, in the face of such apparently insoluble difficulty, Newell remains confident that "properly conceived and diagnosed, palaeontological species and subspecies can be consistently recognized and studied by the same methods as those employed in neontology."[57] How does he imagine this might be possible?

The answer, Newell determines, is to apply quantitative analysis to the confusing array of fossil data—to let statistics do what the paleontologist is unable to accomplish using traditional, descriptive techniques. In the past, paleontologists had relied on a typological basis for identifying species and higher taxa, but ecological and evolutionary study requires paleontology to reorient itself to the neontological population understanding; according to Newell, the "crude procedure" of typology "does not measure up to modern requirements in studies of stratigraphic and evolutionary palaeontology."[58] This is mainly because the typological species concept ignores population variability, which should in each instance follow a normal population curve. A type specimen is normally chosen (i.e., sampled) arbitrarily, and the paleontologist has no guarantee that it "represent[s] the most frequent condition of populations" (i.e., that it would fall in the middle of a normal variability curve). Instead, the procedure should be to select, ideally as randomly as possible, a group of examples from a population and to estimate, using "biometrical analysis," the range of variation for that population. The trick, according to Newell, "is to summarise in a reasonably accurate way the characteristics of a vast assemblage of individuals, perhaps numbering billions, by means of data provided by a few specimens."[59]

The only way such a drastic extrapolation is justified is if we can have confidence that the few specimens chosen give a reasonable indication of the limits of variability in their parent population. Surprisingly, Newell argues, most populations *can* be estimated in such a way, and individual samples are in fact reliable indicators of average variability, provided that they are sampled *randomly*. The mistaken belief that only large and well-documented collections can be analyzed this way has meant "very little headway has been made toward the establishment of uniform practice in quantitative palaeontology"; what we are seeing in Newell's proposal is the solidification of a major argument that statistical analysis can correct for the inadequacies of fossil preservation. This would be perhaps the single most important future direction in paleobiology, but it ultimately depended on a serendipitous convergence of paleontological thinking and technology. As Newell noted several years later, "the recent application of electronic IBM computers in the solution of paleontologic problems" is "more than just another statistical technique"; rather, as Newell went on to predict, the advent of inexpensive, readily available digital computing meant that "in the near future, we may have at our disposal the means for more or less routine quantitative solutions of all sorts of paleontological problems involving complex interrelationiships of many variables."[60] In other words, evolutionary paleontology was about to become a quantitative discipline.

In Newell's second major area of contribution—the study of mass extinctions—he set out to examine patterns in the invertebrate fossil record with a particular eye for relationships between organic and physical histories, and his work directly influenced some of the most important paleobiological theories of the next generation. In the first of three important papers, "Catastrophism and the Fossil Record," published in *Evolution* in 1956, Newell addressed German paleontologist Otto Schindewolf's arguments about "the enigmatic, apparently world-wide, major interruptions in the fossil record which mark the boundaries of the eras."[61] In granting that "abrupt paleontological changes at these stratigraphic levels are real, [and] apparently synchronous," Newell helped to legitimize the study of mass extinctions as a significant evolutionary process, and provided important groundwork for David Raup and Jack Sepkoski's later analysis of mass extinction patterns. This legitimization was important: up until the time of Newell's essays, the prevailing attitude in the paleontological community was that to seriously discuss the possibility of cyclical mass extinctions was to invoke the specter of catastrophism, which was associated either with old, discredited ideas, or with the lunatic fringe. But in even being willing to discuss catastrophism publicly Newell was taking a brave stand, and his series of papers may have helped erase some of the taint that surrounded discussion of mass extinctions.

A fairly definitive statement of Newell's understanding of the role of mass extinctions in evolutionary history can be seen in two of his later essays on the subject: a paper on "Revolutions and the History of Life" delivered at a special Geological Society of America symposium in 1963, and a more popular piece published in *Scientific American* the same year.[62] Newell's symposium paper opens with the bold claim that "the purpose of this essay is to demonstrate that the history of life . . . has been episodic rather than uniform, and to show that modern paleontology must incorporate certain aspects of both catastrophism and uniformitarianism while rejecting others."[63] Noting that most geologists think "change" is "uniform and predictable rather than variable and stochastic," he calls for greater openness toward discontinuity and unpredictability, and opines that "catastrophism rightly emphasized the episodic character of geologic history, the rapidity of some changes, and the difficulty of drawing exact analogies between past and present."[64] This statement is a fairly remarkable repudiation of the ubiquity of uniformitarianism, a pillar of both Darwin's theory and the neo-Darwinian interpretation of the Modern Synthesis, and Newell makes it clear that he intends it as such. A major assumption of uniformitarianism is that gaps in the fossil record are the result of biases in deposition, preservation, or collection, but here Newell endorses Schindewolf's argument that when such "abrupt changes occur in relatively complete sequences over a large part of the earth, they indicate episodes of greatly increased rate of extinction and evolution."[65] He also points to other factors, such as the stratigraphic correlation of extinctions of totally unrelated groups, and the tendency for episodes of apparent extinction to be followed by evidence of "episodes of exceptional radiation." This latter point is especially important, since it contributes to a model of how extinction and evolution function hand in glove: Newell proposes that major extinction events clear the adaptive landscape and open new niches for surviving organisms to exploit, leading to massive and relatively sudden migrations and the production of new forms.[66]

This paper also includes a lengthy consideration of causal factors in mass extinctions, and here Newell presses more urgently the need to develop explanations for the regular extinction of unrelated groups. After first dismissing proposed causes such as cosmic radiation, oxygen fluctuations, changes in ocean salinity, and saltation, he presents a tentative hypothesis of selective elimination via environmental change as the major cause of mass extinction. According to Newell, "this hypothesis postulates widespread, approximately synchronous, environmental disturbances and greatly increased selection pressure," for which he suggests three possible causes.[67] The first of these is migrations "involving better adapted immigrants and less adapted natives," which might become more frequent during times of environmental stress. This he poses as a direct challenge to Darwin's assertion that migrations are "selective and continuous," although he notes this is probably the least likely source of very sharp discontinuities in the fossil record. The second factor is "severe climate changes," such as global ice ages, but while Newell observes this has been the most popular explanation for major extinctions (e.g., the dinosaurs) he discounts its importance since (a) evidence of major climate shifts does not correspond with extinction events, and (b) plants (which we would expect to be especially responsive to climate fluctuations) are not affected during major mass extinctions of animals.[68] Finally, he addresses paleogeographic factors such as changes in sea level, which unsurprisingly emerge as the most likely culprit. According to Newell "it seems clear that rapid emergence of the continents would result in catastrophic changes in both terrestrial and marine habitats and such changes might well trigger mass extinctions among the most fragile species."[69]

Overall, Newell's contributions to the study of mass extinction are significant primarily because of their legitimizing factor within the discipline. While sea level is no longer considered a major factor in the most dramatic extinction events in the history of life, Newell, as a past president of the Paleontological Society and a widely respected figure in the field, lent considerable respectability to this area of study. By challenging some of the tenets of uniformitarianism, he also opened the door to more radical critiques of neo-Darwinism presented by paleobiologists over the next two decades. Indeed, two of the more active proponents of such revisions were directly influenced by Newell: Gould was Newell's doctoral student at Columbia between 1963 and 1967, and Niles Eldredge studied with Newell throughout the 1960s as both an undergraduate and a graduate student. As Eldredge recalls, it was not lost on either Gould or himself that "Newell was the only person in twentieth century paleontology who was talking about the importance of extinction," a fact that led directly to Eldredge's own interest in patterns of evolution and extinction.[70] Perhaps even more importantly, however, Newell stressed that characterizing evolution and extinction as episodic, discontinuous, and stochastic did not mean abandoning a quest for general regularities, nor did it necessitate abandoning a systematic, quantitative study of the fossil record. As he put it, "yet the record of past revolutions in the animal kingdom is understandable by application of basic principles of modern science. In this sense, the present is the key to the past."[71] As many of the chapters in this volume will explore, one of the central themes in the modern paleobiological movement would be the explainability—and even predictability—of complex, dynamic phenomena such as evolution and extinction. And in this regard most of the paleontologists at the forefront of this research over the next two decades were, either directly or indirectly, Newell's students.

THE PALEOBIOLOGICAL REVOLUTION

Between roughly 1970 and 1985, paleobiology went through what might properly be called a revolution, which saw the goals and methods of theoretically minded, biologically oriented paleontology promoted on a wider stage than ever before. As this period of paleobiology's history is the central subject of this book, I will let the following chapters speak for themselves. However, broadly speaking, beginning in about 1970, paleobiology entered its more active proselytizing phase, and paleobiologists self-consciously worked to raise the status of their discipline, both by promoting the theoretical products of quantitative, theoretical paleontology, and by establishing new institutional and disciplinary footholds, including pedagogical reform and the establishment of new outlets for publication. From an intellectual perspective, the most spectacular example was Gould and Eldredge's "Punctuated Equilibria: An Alternative to Phyletic Gradualism," which appeared in 1972 in a collection of essays entitled *Models in Paleobiology*, edited by Thomas J. M. Schopf. This work was joined by studies by Raup, Steven Stanley, Sepkoski, and others, of species diversity, taxonomic survivorship, and rates of evolution and extinction using stochastic (random) modeling and multivariate analysis to fundamentally reorient many of the questions paleontologists were asking about the nature of evolutionary change. These studies were based on techniques that were not part of typical graduate education in paleontology, and required their authors to cross disciplinary boundaries to import new methodologies.

In particular, paleobiologists drew heavily on statistical techniques developed during the previous few decades in population biology, which had undergone a kind of quantitative revolution of its own in the 1950s and early 1960s. A transitional moment for paleobiologists also came in 1975, when a new journal—titled simply *Paleobiology*—was launched by the Paleontological Society, under the guidance of Schopf, who served as editor until 1980. The explicit intention behind this journal was to promote new paleontological methods and questions, and from its inception it served as the primary organ for quantitative studies in macroevolution and extinction. Another, equally important role the journal played, however, was as a mouthpiece for manifestos promoting the new agenda. Gould, in particular, published a number of essays of a general, theoretical nature touting the significance of his approach to evolutionary modeling in the first ten years of the journal's existence.

The early 1980s saw the establishment of paleobiology as a mainstay in many university and museum departments, and the contributions of paleontologists to evolutionary theory became standard literature in evolutionary biology. However, its status was not uncontested, and this volume offers perspectives on several key debates within paleobiology. One locus for controversy was Gould's promotion of a purportedly non-Darwinian, antiadaptationist program, which drew fire from biologists and paleontologists alike. Even as it drove innovative studies of the patterns and processes involved in macroevolution, the work of Gould, Eldredge, Stanley, and others provoked controversy in many quarters. While this debate took place in a variety of forums (including journal publications and correspondence), a central event that is examined is the notorious macroevolution conference that took place in 1980 at the Field Museum of Natural History in Chicago, where paleontologists and biologists clashed over the interpretation of punctuated equilibrium and other macroevolutionary hypotheses advanced by paleontologists. A second major topic of controversy during the 1980s were studies of mass extinction, authored by Raup and Sepkoski, that used statistical analysis to propose a twenty-six-million-year cycle of periodic mass extinctions in the fossil record. This work was closely tied to the discovery, by Louis and Walter Alvarez, of physical evidence of the impact event that may have killed off the dinosaurs, and to the wider (and more controversial) Nemesis or death star hypothesis. Macroevolution and mass extinction became the signature themes of recent paleobiology, and they were also the topics of greatest controversy.

But as this introductory essay has argued, the rapid development of paleobiology over the past several decades was preceded by a less visible, but vitally important, period when paleobiology began to emerge from traditional descriptive paleontology. I have focused particularly on the work of G. G. Simpson and Norman Newell, two of the most active early promoters of paleobiology, but I might have just as easily focused on other, equally important developments, including the growth of paleoecology during the 1960s, the role of non-English language paleontological theory (such as the German "morphological tradition" discussed by Laubischler and Niklas in this volume), the advent of mathematical models and computing technology, the discovery of Precambrian fossils, the authorship of textbooks, the proliferation of journals, or any of a variety of additional topics. The chapters that follow offer additional perspectives on the history and philosophy of paleobiology, including first-hand accounts by several of the leading figures of the paleobiological revolution, which shed light on many of these issues. The point is that modern paleobiology has important antecedents in earlier lines of intellectual and institutional development, all of which are necessary to understand why paleobiology exists in the form it does today, and, as a continually evolving scientific discipline, where it may lead in the future.

NOTES

1. Roger J. Lincoln, Geoffrey Allan Boxshall, and P. F. Clark, *A Dictionary of Ecology, Evolution, and Systematics*, 179.

2. See David Sepkoski, "The 'Delayed Synthesis': Paleobiology in the 1970s," in *Descended from Darwin: Insights into American Evolutionary Studies, 1925–1950*, ed. Joseph Cain and Michael Ruse. Forthcoming.

3. See, e.g., Elizabeth B. Gasking, *The Rise of Experimental Biology;* Garland E. Allen, *Life Science in the Twentieth Century;* Philip J. Pauly, *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology*.

4. See particularly Peter J. Bowler, *The Mendelian Revolution: The Emergence of Hereditarian Concepts in Modern Science and Society*.

5. William Coleman, *Biology in the Nineteenth Century: Problems of Form, Function, and Transformation*, 66.

6. See Ronald Rainger, "Subtle Agents for Change: The Journal of Paleontology, J. Marvin Weller, and Shifting Emphases in Invertebrate Paleontology, 1930–1965."

7. See Peter J. Bowler, *Life's Splendid Drama: Evolutionary Biology and the Reconstruction of Life's Ancestry, 1860–1940*.

8. Vassiliki Betty Smocovitis, *Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology*, 122 and 127.

9. For the history of population genetics, see William B. Provine, *The Origins of Theoretical Population Genetics*.

10. S. S. Buckman, *Quarterly Journal of the Geological Society* 49 (1893), 127. The *Oxford English Dictionary* records this as the first appearance of the word. It is possible that the term has an earlier, independent origin, but no earlier usage has been established.

11. W. E. Reif, "The Search for a Macroevolutionary Theory in German Paleontology," *Journal of the History of Biology* 19 (1986); W. E. Reif, "Deutschsprachige Paläontologie Im Spannungsfeld Zwischen Makroevolutionstheorie Und Neo-Darwinismus (1920–1950)," in *Die Entstehung Der Synthetischen Theorie. Beitruage Zur Geschichte Der Evolutionsbiologie in Deutschland 1930–1950*, ed. T. Junker and E.-M. Engels.

12. Bowler, *Life's Splendid Drama*, 359.

13. Othenio Abel, *Palaeobiologie Und Stammesgeschichte*, 399. All translations are mine unless otherwise noted.

14. Ibid., v.

15. Ibid., 5.

16. Ibid., vi.

17. George Gaylord Simpson, *Tempo and Mode in Evolution*, 149.

18. George Gaylord Simpson, "Mesozoic Mammalia, IV; the Multituberculates as Living Animals," *American Journal of Science* 11 (1926) 228.

19. Simpson, quoted in Ernst Mayr and William B. Provine, *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, (Cambridge, MA: Harvard University Press, 1980), 456. See Othenio Abel, *Grundzëuge der Palaeobiologie der Wirbeltiere*, (Stuttgart,: E. Schweizerbart, 1912).

20. U. Kutschera, "Palaeobiology: The Origin and Evolution of a Scientific Discipline," *Trends in Ecology and Evolution* 22, no. 4 (2007).

21. Ronald Rainger, "Vertebrate Paleontology as Biology: Henry Fairfield Osborn and the American Museum of Natural History," in *The American Development of Biology*, ed. Ronald Rainger, 1988, 244.

22. Prominent histories of the synthesis include *Provine, The Origins of Theoretical Population Genetics; Smocovitis, Unifying Biology; Mayr and Provine, The Evolutionary Synthesis: Perspectives on the Unification of Biology; Ernst Mayr, The Growth of Biological Thought: Diversity, Evolution, and Inheritance;* Joseph A. Cain, "Common Problems and Cooperative Solutions: Organizational Activity in Evolutionary Studies, 1936–1947," *Isis* 84 (1993); Joseph A. Cain, "Epistemic and Community Transition in American Evolutionary Studies: The 'Committee on Common Problems of Genetics, Paleontology, and Systematics' (1942–1949)," *Studies in History and Philosophy of Biological and Biomedical Sciences* 33 (2002); and Allen, *Life Science in the Twentieth Century.*

23. Some historians, including Provine, view this as *the* major accomplishment of the synthesis. Provine, *The Origins of Theoretical Population Genetics*,

24. Patricia M. Princehouse, "Mutant Phoenix: Macroevolution in Twentieth-Century Debates over Synthesis and Punctuated Evolution" (PhD diss., Harvard University, 2003), 21.

25. Simpson, quoted in Ernst Mayr, "G. G. Simpson," in *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, ed. Ernst Mayr and William B. Provine, 455.

26. George Gaylord Simpson and Anne Roe, *Quantitative Zoology; Numerical Concepts and Methods in the Study of Recent and Fossil Animals*, 1st ed., vii.

27. Simpson and Roe, *Quantitative Zoology*, viii.

28. Simpson, *Tempo and Mode in Evolution*, vi.

29. Simpson, quoted in Mayr, "G. G. Simpson," 456.

30. Simpson, quoted in Leo F. Laporte, *George Gaylord Simpson: Paleontologist and Evolutionist*, 25.

31. Simpson, *Tempo and Mode in Evolution*, xvi.

32. Ibid., 206.

33. Ibid., 97.

34. Stephen Jay Gould, "G. G. Simpson, Paleontology, and the Modern Synthesis," in *The Evolutionary Synthesis; Perspectives on the Unification of Biology*, ed. Ernst Mayr and W. B. Provine, 161.

35. Simpson, *Tempo and Mode in Evolution*, 98.

36. Ibid., 99.

37. Ibid., 107.

38. Gould, "G. G. Simpson, Paleontology, and the Modern Synthesis," 158–59.

39. See Raymond Pearl and Lowell J. Reed, "On the Rate of Growth of the Population of the United States since 1790 and Its Mathematical Representation," *Proceedings of the National Academy of Sciences of the United States of America* 6, no. 6 (1920).

40. Simpson, *Tempo and Mode in Evolution*, 24–26.

41. J. Brookes Knight, "Paleontologist or Geologist," *Bulletin of the Geological Sociey of America* 58 (1947) 282–83.

42. J. Marvin Weller, "Relations of the Invertebrate Paleontologist to Geology," *Journal of Paleontology* 21, no. 6 (1947) 570. See also Rainger, "Subtle Agents for Change."

43. Weller, "Relations of the Invertebrate Paleontologist to Geology," 572.

44. Stephen Jay Gould to Niles Eldredge, March 9, 1978. American Museum of Natural History (AMNH) Invertebrates Department Archive.

45. Preston Cloud to Roger Batten, February 22, 1978. AMNH Invertebrates Archive.

46. Ernst Mayr to Niles Eldredge, March 1, 1978. AMNH Invertebrates Archive.

47. Norman Dennis Newell and Edwin Harris Colbert, "Paleontologist; Biologist or Geologist," *Journal of Paleontology* 22, no. 2 (1948) 265.

48. Newell and Colbert, "Paleontologist; Biologist or Geologist," 267.

49. Norman Newell, "Instruction in Paleobiology," American Museum of Natural History Department of Vertebrate Paleontology Archive (n.d.), Box 67, Folder 21.

50. Norman Dennis Newell, "Adequacy of the Fossil Record," *Journal of Paleontology* 33, no. 3 (1959) 489.

51. Ibid., 490.

52. Ibid., 490–91.

53. Newell, "Adequacy of the Fossil Record," 492; Charles Schuchert, "Biologic Principles of Paleogeography," *Popular Science* (1910) 591–92; Curt Teichert, "How Many Fossil Species?" *Journal of Paleontology* 30, no. 4 (1956).

54. Newell, "Adequacy of the Fossil Record," 499.

55. Norman D. Newell, "Fossil Populations," in *The Species Concept in Palaeontology: A Symposium*, ed. P. C. Sylvester-Bradley, 67.

56. Ibid., 70.

57. Ibid., 70–71.

58. Ibid., 71.

59. Ibid., 74.

60. Newell, "Adequacy of the Fossil Record," 490.

61. Norman Dennis Newell, "Catastrophism and the Fossil Record," *Evolution* 10, no. 1 (1956a) 97.

62. Norman D Newell, "Revolutions in the History of Life," in *Uniformity and Simplicity. Special Paper–Geological Society of America;* Norman D Newell, "Crises in the History of Life," *Scientific American* 208, no. 2 (1963). Because the two pieces were composed at the same time and cover substantially similar topics, reference here will be made only to the more scholarly presentation from the GSA symposium.

63. Ibid., 64.

64. Ibid., 65.

65. Ibid., 74.

66. Ibid., 82.

67. Ibid., 84.

68. Ibid., 85.

69. Ibid., 88.

70. Interview with Niles Eldredge, conducted by David Sepkoski, 1/19/06. Transcript in author's possession.

71. Newell, "Revolutions in the History of Life," 89.

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