An engaging area of biology for more than a century, the study of macroevolution continues to offer profound insight into our understanding of the tempo of evolution and the evolution of biological diversity. In seeking to unravel the patterns and processes that regulate large-scale evolutionary change, the study of macroevolution asks: What regulates biological diversity and its historical development? Can it be explained by natural selection alone? Has geologic history regulated the tempo of diversification? The answers to such questions lie in many disciplines including genetics, paleontology, and geology.

This expanded and updated second edition offers a comprehensive look at macroevolution and its underpinnings, with a primary emphasis on animal evolution. From a neo-Darwinian point of view, it integrates evolutionary processes at all levels to explain the diversity of animal life. It examines a wide range of topics including genetics and speciation, development and evolution, the constructional and functional aspects of form, fossil lineages, and systematics. This book also takes a hard look at the Cambrian explosion. This new edition possesses all of the comprehensiveness of the first edition, yet ushers it into the age of molecular approaches to evolution and development. It also integrates important recent contributions made to our understanding of the early evolution of animal life. Researchers and graduate students will find this insightful book a most comprehensive and up-to-date examination of macroevolution.

Jeffrey S. Levinton is a professor in the Department of Ecology and Evolution at the State University of New York at Stony Brook.
For Joan, always

Such stillness –
The cries of the cicadas
Sink into the rocks
– Matsuo Basho, The Narrow Road of Oku

Life don’t clckety clack down a straight line track
It come together and it come apart.
– Ferron, 1996
## Contents

<table>
<thead>
<tr>
<th>Chapter</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Preface to the First Edition</td>
<td>ix</td>
</tr>
<tr>
<td>Preface to the Second Edition</td>
<td>xiii</td>
</tr>
<tr>
<td>1 Macroevolution: The Problem and the Field</td>
<td>1</td>
</tr>
<tr>
<td>2 Genealogy, Systematics, and Macroevolution</td>
<td>32</td>
</tr>
<tr>
<td>3 Genetics, Speciation, and Transspecific Evolution</td>
<td>81</td>
</tr>
<tr>
<td>4 Development and Evolution</td>
<td>157</td>
</tr>
<tr>
<td>5 The Constructional and Functional Aspects of Form</td>
<td>227</td>
</tr>
<tr>
<td>6 Patterns of Morphological Change in Fossil Lineages</td>
<td>285</td>
</tr>
<tr>
<td>7 Patterns of Diversity, Origination, and Extinction</td>
<td>367</td>
</tr>
<tr>
<td>8 A Cambrian Explosion?</td>
<td>443</td>
</tr>
<tr>
<td>9 Coda: Ten Theses</td>
<td>495</td>
</tr>
<tr>
<td><strong>Glossary of Macroevolution</strong></td>
<td>511</td>
</tr>
<tr>
<td><strong>References</strong></td>
<td>519</td>
</tr>
<tr>
<td><strong>Author Index</strong></td>
<td>587</td>
</tr>
<tr>
<td><strong>Subject Index</strong></td>
<td>605</td>
</tr>
</tbody>
</table>
Preface to the First Edition

I have so many things to write about, that my head is as full of oddly assorted ideas, as a bottle on the table is filled with animals.

– Charles Darwin, 1832, Rio de Janeiro

Evolutionary biology enjoys the peculiar dual status of being that subject which clearly unites all biological endeavors, while occasionally seeming to be nearly as remote from complete understanding as when Darwin brought it within the realm of materialistic science. Somehow, the basic precepts first proposed by Darwin have never been either fully accepted or disposed, to be followed by a movement toward further progress in some other direction. The arguments of today – the questions of natural selection and adaptation, saltation versus gradualism, and questions of relatedness among organisms – are not all that different from those discussed 100 years ago, even if the research materials seem that much more sophisticated.

Darwin espoused thinking in terms of populations. His approach was open to experimentation, but this had to await the (re)discovery of genetics half a century later, before a major impediment to our understanding could be thrown aside. As it turned out, the rediscovery of genetics was initially more confusing than helpful to our understanding of evolution. The rediscovery of genetically transmissible discrete traits revived saltationism, and it took over a decade for biologists to realize that there was no conflict between the origin of discrete variants and the theory of natural selection. In the twentieth century, the focus of experimentalists moved toward processes occurring within populations. But many of the inherently most fascinating questions lie at higher taxonomic levels, or at greater distances of relationship than between individuals in a population. The questions are both descriptive and mechanistic. We would like to know just how to describe the difference between a lizard and an elephant, in terms that would make it possible to conceive of the evolutionary links between them. We are only now beginning to do this, principally at the molecular genetic level. Differences in nucleotide sequences are beginning to have more meaning at this level, especially because of the emerging knowledge of gene regulation. But we would also like to understand the mechanisms behind the evolutionary process at higher levels of morphological organization. This inevitably
involves a knowledge of history with all the limitations that that subject embraces. Just how can we be sure about biological historical facts? Surely the fossil record must come into play here, even if it is scattered in preservation.

I will try here to provide an approach to studying macroevolution, which I define to be the study of transitions between related groups of distant taxonomic rank. The formula is simple. First, we must have a sound systematic base that is derived from a well-established network of genealogical relationships. Otherwise, we cannot ask the appropriate questions in the first place. Second, we must be able to describe the differences between organisms in molecular, developmental, morphological, and genetic terms. Third, we must understand the processes of evolution at all levels, from the nature of polymorphisms to the appearance and extinction of major groups. Finally, we must have a criterion by which adaptation can be judged. It may not be true that one group is inherently superior to another unrelated group. But if we cannot devise a criterion for increases in performance, even in biologically complex organisms, then we will not be able to test Darwin's claim that evolution involves improvement (not perfection) in a given context of an organism–environment relationship.

Because the problems require such a broad scope of approaches and solutions, our understanding of macroevolution is often mired in arguments that appear, then disappear, then reappear, with no real sense of progress. The saltationist–gradualist argument has had such a history, simply because of our lack of knowledge as to what saltation really means and the usual lack of a good historical record. Because evolutionary biologists tend to reason by example, it is easy to “prove a point” by citing a hopelessly obscure case or one that may turn out to be unusual. Yet it seems fruitless to settle an argument by counting up all of the examples to prove a claim, without some theoretical reason to expect the majority of cases to fit in the first place. This danger is endemic to a science that depends on history. Most biologists would be quite disappointed if evolutionary biology were nothing much more than a form of stamp collecting. We look for theories and principles.

It is my hope that this volume will provide a framework within which to view macroevolution. I don’t pretend to solve the important issues, but I do hope to redirect graduate students and colleagues toward some fruitful directions of thought. Although I like to think that this is a balanced presentation, my shortcomings and prejudices will often surface. In particular, this volume will resort to advocacy when attacking the view of evolution that speciation is a fundamental level of evolutionary change in the macroevolutionary perspective, and that the neo-Darwinian movement and the Modern Synthesis somehow undermined our ability to understand the process of evolution and brought us to our present pass of misunderstanding. The recent “born again” moves toward saltationism, and the staunchly ideological adherence to related restrictive concepts, such as punctuated equilibria, are great leaps backward and have already led many toward unproductive dead ends that are more filled with rhetoric than scientific progress. Ultimately this is a pity, because some of these ideas have been interesting and have exposed unresolved issues in evolutionary theory.

Although this book is principally meant to be a blueprint for the study of macroevolution, I found it necessary to discuss certain areas at an elementary level.
This is partially owing to the heterogeneous audience that I anticipate. I doubt that most paleontologists will be aware of the details of genetics, and neontologists will similarly benefit from some geological introduction.

Many colleagues were very generous with their time in reviewing this manuscript. I thank the following who reviewed one or more chapters: Richard K. Bambach (chapters 1–8), Michael J. Bell (chapters 3, 4, 7), Stefan Bengtson (chapters 7, 8), John T. Bonner (chapters 1–8), Peter W. Bretsky Jr. (chapters 7, 8), Brian Charlesworth (chapters 3, 7, 8), John Cisne (chapter 7), Richard Cowan (chapters 6, 7), Gabriel Dover (part of chapter 3), Walter Eanes (chapters 3, 4), Joseph Felsenstein (chapter 2), Karl Flessa (chapter 8), Douglas Futuyma (chapters 1, 3, 4), Paul Harvey (part of chapter 6), Max Hecht (chapters 1–8), George Lauder (chapter 6), Jack Sepkoski (chapter 8), David Wake (chapter 5), and especially David Jablonski (chapters 1–9). This sounds like extensive reviewing, but consider my extensive ignorance.

I also have been lucky to have had conversations or correspondence with many individuals who gave me useful information, their unpublished works, letters, insights, and important references. Among them, I am grateful to Bill Atchley, David Wake, Björn Kurttén, Lars Werdelin, Steve Orzack, John Maynard Smith, Brian Charlesworth, Michael Bell, Pete Bretsky, Gabriel Dover, Steve Farris, Steve Stanley, Doug Futuyma, Walter Eanes, Curt Teichert, George Oster, Richard Reymenl, Jürgen Schöbel, Max Hecht, Russell Lande, Art Boucot, Ledyard Stebbins, Vjalda Jaanusson, Ernst Mayr, George Gaylord Simpson, Jack Sepkoski, and Urjö Haila.

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Banyuls-Sur-Mer and Stony Brook
Preface to the Second Edition

In the past decade, my vision of macroevolution has taken hold and will dominate macroevolutionary thinking in the next decade as well, although I can hardly say that I had much to do with its ascent. I defined macroevolution to be the sum of those processes that explain the character-state transitions that diagnose evolutionary differences of major taxonomic rank. I focused on the individual, development, and models explaining the evolution of form. Previously, the definition that held sway was: evolution above the species level. This is not just a definition: It directed macroevolutionary studies to speciation rates, the importance of speciation, and even models that argue that something about the speciation process is the motor of morphological evolution.

The focus on above-species-level processes has given us some very exciting results, such as the late Jack Sepkoski’s relentless pursuit of a large-scale data base to provide a biodiversity thermometer for earth processes. But it leaves out much; I would say it omits the most interesting stuff. I would say that models emphasizing speciation and sorting among species have proven unimportant, even if the obvious effects of extinction as a filter are still self-evident.

In the past decade, the field has diverted strongly to studies that explain character transformation. This has been aided by the entry of phylogenetic methods in paleontological studies. Sure, there were a few phylogenetic studies done with fossil groups before 1990, but now they are dominant. Indeed, some phylogenetic systematists actively forestalled the use of fossil groups in constructing phylogenies, but paleontologists came back and even successfully introduced stratigraphic order of appearance as a credible approach to tree construction. This has led to an appreciation of character transformations and their mapping to phylogenies. At this juncture, paleontologists simply dominate the field in studies of large-scale radiations (e.g., animals, mammals) and have mounted credible attacks of neontological tools (e.g., molecular estimates of divergence times).

A revolution in the study of developmental genes has also transformed our understanding of character transformation. For the first time, the basic organization of an animal embryo is beginning to be understood in terms of gene action and we are beginning to be able to connect these genes with developmental processes known traditionally from embryology. We even can now connect variation in gene action
with polymorphism, which makes developmental gene studies accessible to population-genetic analyses. The decade of developmental gene discovery will lead to a next decade of increasing connection of morphology to gene action and genetic variation. The past decade witnessed the rise of so-called devo-evo approaches. In the next decade, this jargon will disappear, as studies linking genes to development will permeate studies of everything from polymorphism to phylogeny.

In the first edition, I suggested that nothing from paleontology will be more exciting than examining the beginning of it all. For animals, this means the Cambrian explosion, of course. No one could have predicted the explosion of discoveries that has amplified the menagerie of Cambrian fossils during the 1990s. We now have Early Cambrian fish, connections between previously poorly understood fossil groups such as the Lobopods, and many more fossil localities, thanks to the searching of a number of astute paleontologists.

For paleontology and evolutionary biology, the issue of time scales reigns supreme, for many of our measures and models of evolution arise from rates. Some paleontological studies have produced elegant estimates of the extent of the missing temporal ranges for fossil groups, the proportion of fossils preserved, and the total biodiversity. Debates on diversity change, rates of diversification, extinctions, and other processes are more productive because they are bound by data constrained by quantitative arguments.

It is also heartening to see the approach of using character transformation as an organizing force in macroevolution; this tends to unify paleontologists and neontologists. In the past, many paleontologists have treated neontologists like the enemy, and vice versa. Paleontologists are needlessly defensive of their admittedly serendipitous profession, where a fossil find in a remote place may turn things upside down. If I put such a wonderful fossil into the hands of most neontologists, would they know what they are looking at? Doubtful, would be my answer. On the other hand, neontologists have nearly unique access to the integration of population-level processes and evolutionary change, not to mention the gene-based approach to be able to explain change mechanistically. Paleontologists are a bit shy about giving credit to the strength of this approach. It is as if someone wants to “win” something, and many otherwise excellent studies are weakened by an obvious defensiveness that is perhaps grounded in an unfounded sense of inferiority.

This edition has a similar structure with a few exceptions. I have eliminated the chapter on genetic variation and have instead moved relevant descriptions of within-population variation studies to other chapters where necessary. The chapter (4) on development and evolution has had to be greatly amplified, owing to the many discoveries of the action of developmental genes. This field is still very primitive and it is likely that the next decade will make hash of many of the current enthusiasms for universal gene controls and other models. Finally, I have added a chapter devoted to the so-called Cambrian Explosion (8). This topic is explosive, even if the event was probably not. I am sure that as soon as I turn this manuscript in, some paper will appear that spins things around. At least I hope so.

The first edition was reviewed by many colleagues before publication and I am still grateful for their comments. Since that time, I have benefited greatly from con-
PREFACE TO THE SECOND EDITION

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