Genetics, Paleontology, and Macroevolution; Second Edition

Jeffrey S. Levinton

CAMBRIDGE UNIVERSITY PRESS

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Second Edition

An engaging area of biology for more then 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.

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PUBLISHED BY CAMBRIDGE UNIVERSITY PRESS (VIRTUAL PUBLISHING)
FOR AND ON BEHALF OF THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge CB2 IRP
40 West 20th Street, New York, NY 10011-4211, USA
477 Williamstown Road, Port Melbourne, VIC 3207, Australia

http://www.cambridge.org

First published in printed format 1988
Second edition 2001

A catalogue record for the original printed book is available
from the British Library and from the Library of Congress
Original ISBN 0 521 80317 9 hardback
Original ISBN 0 521 00550 7 paperback

ISBN 0 511 01829 0 virtual (netLibrary Edition)

For Joan, always

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

Life don't clickety clack down a straight line track
It come together and it come apart.
– Ferron, 1996

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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 Kurtén, 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 Reyment, Jürgen Schöbel, Max Hecht, Russell Lande, Art Boucot, Ledyard Stebbins, Vjaldar Jaanusson, Ernst Mayr, George Gaylord Simpson, Jack Sepkoski, and Urjö Haila.

The manuscript for this book was prepared using the Document Composition Facility at the Biological Science Computing Facility at the State University of New York at Stony Brook. I am very grateful to Dave Van Voorhees, who, in the main, formatted the manuscript into appropriate files. Scott Ferson, Kent Fiala, and Jim Rohlf were infinitely patient with our questions, and all contributed materially to our ability to produce the final product. I am also very grateful to Mitzi Eisel and to Marie Gladwish for skillfully preparing most of the figures. I also thank Richard Ziemacki, Helen Wheeler, Jim DeMartino, Peter-John Leone, and especially Rhona Johnson, all of Cambridge University Press, for their patience and kindness. Most of all I am grateful to my wife Joan, who made life so easy (at least for me) while I prepared the manuscript.

I am very grateful for the hospitality of Staffan Ulfstrand, Zoology Department of the University of Uppsala; Gabriel Dover of the Department of Genetics at Kings College, University of Cambridge; Catherin Thiriot, Odile Mayzaud, and Patrick Mayzaud, all of the Station Zoologique, Villefranche-Sur-Mer, France; and Jacques Soyer, Laboratoire Arago, Banyuls-Sur-Mer, France. I also am deeply grateful to the Guggenheim Foundation, which mainly supported the writing of this work.

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 conversations with many others, perhaps too many to cite them by name. I do feel compelled to mention Tony Hoffman and Jack Sepkoski, both who have left us far before their time. This revision was completed at the Centre for the Study of Ecological Impacts of Coastal Cities at the University of Sydney and I am grateful to its director, A. J. Underwood, who gave me a place to stay and a stimulating environment. I also am grateful to all who talk to me in the hallways of my home department at the State University of New York at Stony Brook. I am also grateful to Ellen Carlin, the Cambridge University Press biology editor, and her staff for seeing this second edition to press. Joan Miyazaki was predictably the perfect partner and helped me in many ways with this project.

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CHAPTER 1

Macroevolution: The Problem and the Field

> The science of life is a superb and dazzlingly lighted hall, which may be reached only by passing through a long and ghastly kitchen.
>
> – Claude Bernard

The Process and the Field of Macroevolution

The return of macroevolution. The field of macroevolution embraces the excitement of seeking an understanding of the breadth of life. We have long desired to know how best to describe the diversity of life's forms and to explain how and why this diversity came to be. No mystery is more intriguing than why we have amoebas and horses, or dandelions and palms. The child's first walk in a meadow, when the child sees flowers and butterflies for the first time, can inspire the same wonder in the most sophisticated biologist walking those same tracks many years later.

We return to this perspective from many quarters of biology and paleontology, after many decades of asking far more restrictive questions that tended to put the process of evolution under a microscope. But now we are stepping back, to take in the broader view. The advances in molecular genetics and developmental biology in recent years have only increased our confidence that the nature of living systems can be understood mechanistically; we can now imagine the possibility of describing the difference between organisms in terms of their genes, gene products, and spatial organization. Such descriptions were beyond our grasp even 10 years ago, but now they are at hand, if still in fragments. The large-scale collation of fossil data and a new understanding of the history of the earth have brought similar increases of confidence among geologists and paleontologists. But we should not overlook some significant changes in fields such as systematics, and the crucial groundwork in population biology established through the advances of the neo-Darwinian movement and the Modern Synthesis. All these place us in position to answer questions that could not even be asked very seriously just a few decades ago.

Definition of the Process of Macroevolution

I define macroevolution to free it from any dependence on specific controversies and, more importantly, to define a field derived from tributaries that have merged from many sources. I define the process of macroevolution to be (Levinton 1983) *the sum of those processes that explain the character-state transitions that diagnose evolutionary differences of major taxonomic rank*. This definition of macroevolution focuses on character-state differences (defined in chapter 2) rather than on jumps, for example, from one taxon to another of great distance. The definition is noncommittal to any particular taxonomic level. I believe that one should eschew definitions of macroevolution such as (1) evolution above the species level (e.g., Eldredge and Cracraft 1980; Stebbins and Ayala 1981) or (2) evolution caused by speciation and selection among species (e.g., Stanley 1979). These definitions presume that major transitions can be analyzed properly only by examining speciation and other processes occurring at the species level and above, and they restrict our views toward alternative hypotheses. Worse than that, these definitions ignore the forest of organismal phenotypic breadth and focus on the trees of just one component of that breadth.

It is not useful to distinguish sharply between microevolution and macroevolution, as I will show in this volume. The taxonomic rank marking any dichotomy between microevolution and macroevolution would depend on the kind of transition being studied. Our impression of "major" degrees of evolutionary change is inherently qualitative and not fixed at any taxonomic rank across all major taxonomic groups. This is apparent when we consider transitions whose importance may rely on many characters, or just one. For the cichlid fishes, a synarthrosis between the lower pharyngeal jaws, a shift of insertion of the fourth levator externus muscles, and the development of synovial joints between the upper pharyngeal jaws and the basicranium may be necessary (but not sufficient) for the morphological diversification of species with differing food collection devices (Liem 1973). On the other hand, the evolution of the mammals involved a large number of integrated physiological and morphological traits, and these were acquired over a long period of time (Kemp 1982). Yet both fall well within the province of macroevolutionary change, because of the potential at least for evolutionary differences spanning large chasms of taxonomic rank.

A second reason for an unrestricted definition of the taxonomic level required to diagnose macroevolutionary change is the variation in higher level taxonomic splitting among major groups (Van Valen 1973a). There is no simple way of drawing an equivalence between families of mammals and mollusks; comparisons of rates of evolution between groups at "comparable" taxonomic levels (e.g., Stanley 1973a) are therefore usually invalid (Levinton 1983; Van Valen 1973a). This point is illustrated well by qualitative studies on hybridity and genetic and phenotypic distance within groups of species of similar taxonomic distance from different phyla. The taxonomist tends to use a qualitative threshold of phenetic difference to define significant evolutionary distance. Thus the ferret and the stoat were placed in different genera, even though they hybridize and produce fertile offspring. Crosses between congeneric species of frogs, however, do not usually produce viable, let alone fertile, offspring.

Perhaps the most unfortunate influence of taxonomic level in restricting our freedom in studying macroevolution is the presumption that crucial characters define specific taxonomic levels. This approach is a major organizing force for systematics today, despite the several decades since the 1970s when cladistic approaches have taken a more pluralistic view of the role of characters in defining evolutionary groups (clades) with common ancestry (see Chapter 2). This permeating influence derives from Cuvier's important notion of subordination of characters, which has survived through the centuries and has led systematists to accept the idea that specific traits define major taxonomic levels. Such thinking leads to unfortunate ideas as the "origin of orders," even though such a taxonomic level has been defined by an arbitrary character type.

The difficulty of gauging macroevolution by taxonomic distance is exacerbated by our current ignorance of the relationship between morphological and genetic divergence among distantly related taxa. By what proportion of the genome do chimpanzees and humans differ? Despite our available estimates of genetic differentiation from sequenced DNA and protein amino acid sequences, allozymes, and karyotypes, we cannot draw a parallel with our knowledge of morphological differences. We are crippled by this ignorance when seeking to judge how "hard" it is for evolutionary transition to take place. What is our standard of difficulty? Genetic? Functional morphological? Developmental? Worse than that, what if interactions among these three occur? At this point, we cannot even easily inject the notion of time in evolution. We may be able to estimate rates of change of a variety of entities (e.g., DNA sequence, body size, and the like), but we have no idea of whether evolution of a complex morphology, such as the rise of mammals, would be astonishing if it happened in one million years, or dizzyingly slow! If the Cambrian Explosion of eumetazoan life occurred in 10 million years, can we say that this was blazing speed or just an ordinary pace? We do not know.

My last justification for a definition based on genetic and phenotypic breadth is that it permits an expansion of previous evolutionary theory to embrace the larger-scale hierarchical processes (see below) and higher-level taxonomic variations previously ignored by the bulk of evolutionary biologists, except in passing or in gratuitous extrapolation from lower taxonomic levels of concern. It is my hope that my definition will eventually not be needed and that "macroevolution" will merge with "microevolution" to become a discipline without a needless dichotomy. The need for a discipline of macroevolution, in my view, is more to sell the expansion of approaches than to necessarily dismiss any previous theory.

The Scope of Macroevolution

The discipline of macroevolution should include those fields that are needed to elucidate the processes involved in accomplishing the change from one taxonomic state to another of significant distance. Macroevolutionary studies all must be organized around several basic questions:

1. How do we establish the phylogenetic relationships among taxa? What is the nature of evolutionary novelty and how do novel characters define the taxa we delineate?

2. How do genetic, developmental, and morphological components channel the course of morphological and genetic evolution?
3. What are the patterns of change and what processes regulate the rate of evolutionary change from one character state to another?
4. What environmental changes regulated the timing of evolutionary radiations and extinctions?
5. What is the role of extinction in the evolutionary potential of newly evolved or surviving groups?
6. What ecological processes regulate morphological and species diversity? To what degree do these effects have evolutionary consequences for any given group?

In the following chapters, I will try to support the following assertions:

1. Systematics is the linchpin of macroevolutionary studies. Without an acceptable network of phylogenetic relationships, it is impossible to investigate the possible paths of major evolutionary change (chapter 2).
2. The nature of evolutionary novelty is probably the most studied and still the most confused element of evolutionary biology. The presence of discontinuity in morphological state can be explained readily using the available data and theory of genetics (chapters 3 and 4). The mechanisms behind the discontinuities are more poorly understood and may relate to a complex interaction between genetic and developmental processes (chapter 4). The epigenetic processes are also subject to genetic control, and thus a spectrum of resultant morphologies can be discontinuous.
3. There is no evidence that morphological evolution is accelerated or associated with speciation, except as an effect of ecologically unique circumstances leading to directional selection. Intraspecific variation during the history of a species is the stuff of interspecific morphological differentiation (chapter 3). When it occurs, intraspecific stasis is affected mainly by gene flow, at a given time and stabilizing selection, over time.
4. Many genetic and epigenetic aspects of development are conserved in evolution. Early development is especially characterized by the use of widely conserved transcription regulators and other regulatory genes. Development, however, is widely labile, as is the order of appearance of expression in developmental genes. Although the expression of developmental genes can be used to trace homologies in closely related forms, developmental genes are a conservative set of elements that can be expressed radically differently in different organisms. Developmental genes are like the musical notes, and the organisms are like rock music, blues, and baroque music. This suggests that there are no profound constraints restricting evolutionary change. Nevertheless, certain early patterns of gene expression were incorporated early in animal evolution and were retained (chapter 5).
5. The nature of form is best understood within the framework of Adolph Seilacher's concept of *Constructional Morphology.* Constructional, Phylogenetic-Developmental, and Functional Morphological factors interact to determine form. This combination tends to make evolutionary pathways often eccentric and not conducive to predictions from "ground up" engineering approaches to optimality. Once historical constraints are recognized, however, optimality approaches can be used to gauge the performance of alternative morphotypes. Indeed, without such an approach, studies of adaptation would be vacuous (chapter 5).

6. Having understood the nature of variation, we find little evidence that the fossil record consists of anything more than the standard variation within populations that can be studied by evolutionary biologists. The process of macroevolution need not invoke paroxysmal change in genetics or morphology. The genetic basis of morphological change, nevertheless, involves a considerable variety of mechanisms. Morphological evolution is not the necessary *consequence* of speciation, though it may be a *cause* of speciation (chapters 3 and 6).
7. Baupläne are evolved piecemeal. Trends leading to complex forms consist of a large number of specific changes acquired throughout the history of the origin of the derived bauplan (chapter 6). Subsequently, however, stability is common. Some trends, such as a general increase in invertebrate predator defense and reductions in variation of morphologies, are probably due, to a degree, to the selective success and extinction of different taxa. Even though speciation rate is not related causally to the origin of the novelty, intertaxon survival, sometimes due to random extinction, has been a crucial determinant of the present and past complexion of the biotic world (chapter 7).
8. Although earth history has had a clear impact on diversification and standing diversity, patterns of taxonomic longevity may have had a distinctly random component. Major differences in biology may have consequences for rates of morphological evolution and speciation, but patterns of distribution within these groups may reflect random appearance–extinction processes (chapter 7).
9. Mass extinctions and radiations are a fact of the fossil record. But both are more easily recognized by changes in the biota than by any recognizable physical events. Means of distinguishing among current hypotheses of regulation of mass extinction and radiation are equivocal at best (chapter 7).
10. The Cambrian Explosion may have involved two phases. Molecular evidence suggests that the major animal groups diverged, perhaps as small-bodied forms or even as ciliated larvalike forms, about 800 to 1,000 million years ago. The sudden appearance of larger skeletonized body fossils and burrows at the beginning of the Cambrian is probably more of an ecologically driven event reflecting the evolution and radiation of crown groups (the modern phyla), rather than a time when the defining traits of the triploblastic metazoa arose, which was probably long over by Cambrian times (chapter 8).

Is macroevolution something apart from microevolution? Richard Goldschmidt instigated the dichotomous approach to macroevolution when he conceived of hopeful monsters that arose by means of speciation events (see below under Hierarchy and Evolutionary Analysis). The modern version of this beginning pictured a decoupling of microevolution from macroevolution (e.g., Stanley 1975), with the species level being the barrier through which any macroevolutionary change must penetrate. Although the specific notion of macromutations is restricted to only a few macroevolutionists (e.g., Gould 1980a), the notion of an evolutionary breakthrough has been associated with speciation events and their frequency. This point of view has made for an unfortunate battle royal, where victory would mean that the opposing group was irrelevant in evolutionary biology. If the microevolutionists win, then there is no such thing as macroevolution. If the macroevolutionists gain favor, then microevolution exists, but it is a minor part of a much larger set of evolutionary constructs. Macroevolutionist claims began by relegating microevolution to the ash heap of history (e.g., Gould 1980a). It made for great sound bites. Subsequent arguments have softened, only emphasizing the expansion of evolutionary theory offered by macroevolutionary considerations (Gould 1982a).

Is the dichotomy very useful? For one group to "win" conveniently ensures the irrelevance of the other to major contributions in evolutionary theory. The focus of this argument is at the speciation threshold of evolution. But I hope that the reader realizes already that there is much more to paleontological and neontological macroevolutionary arguments than the nature of speciation.

The focus of macroevolution. Macroevolution must be a field that embraces the ecological theater, including the range of time scales of the ecologist, to the sweeping historical changes available only to paleontological study. It must include the peculiarities of history, which must have had singular effects on the directions that the composition of the world's biota took (e.g., the splitting of continents, the establishment of land and oceanic isthmuses). It must take the entire network of phylogenetic relationships and superpose a framework of genetic relationships and appearances of character changes. Then the nature of constraint of evolutionary directions and the qualitative transformation of ancestor to descendant over major taxonomic distances must be explained.

The macroevolutionary foci I mention have been largely ignored by the founders of the Modern Synthesis in the past 50 years, who have been devising theories explaining changes in gene frequencies or small-scale evolutionary events, leaving it to someone else to go through the trouble of working in larger time scales and considering the larger historical scale so important to the grand sweep of evolution within sight of the horizon of the paleontologist. The developmental/genetic mechanisms that generate variation (what used to be called physiological genetics) have also been neglected until recently. Population geneticists assume variation but do not study how it is generated nearly as much as they worry about the fate of variation as it is selected, or lost by stochastic processes.

Evolutionary biology and astronomy share the same intellectual problems. Astronomers search the heavens, accumulate logs of stars, analyze various energy spectra, and note motions of bodies in space. A set of physical laws permits interpretations of the present "snapshot of the universe" afforded by the various telescopic techniques available to us. To the degree that the physical laws permit unambiguous interpretations, conclusions can be drawn about the consistency of certain observations with hypotheses. Thus, rapid and cyclical changes in light intensity led to the proof of the reality of pulsars. The large-scale structure of the universe inspired a more historical hypothesis: the big bang origin of the universe.

Does the evolutionary biologist differ very much from this scheme of inference? A set of organisms exists today in a partially measurable state of spatial, morphological, and chemical relationships. We have a set of physical and biological laws that might be used to construct predictions about the outcome of the evolutionary process. But, as we all know, we are not very successful, except at solving problems at small scales. We have plausible explanations for the reason why moths living in industrialized areas are rich in dark pigment, but we don't know whether or why life arose more than once or why some groups became extinct (e.g., the dinosaurs) whereas others managed to survive (e.g., horseshoe crabs). Either our laws are inadequate and we have not described the available evidence properly or no laws can be devised to predict uniquely what should have happened in the history of life. It is the field of macroevolution that should consider such issues. For better or worse, macroevolutionary biology is as much historical as is astronomy, perhaps with looser laws and more diverse objectives. If history is bunk, then macroevolutionary studies are ... well, draw your own conclusions!

Indeed, the most profound problem in the study of evolution is to understand how poorly repeatable historical events (e.g., the trapping of an endemic radiation in a lake that dries up) can be distinguished from lawlike repeatable processes. A law that states *an endemic radiation will become extinct if its structural habitat disappears* has no force because it maps to the singularity of a historical event. It is how we identify such events that matters. What we cannot do is infer that all unexplainable phenomena arise from such unique events. For example, if we postulate natural selection as the shaping force of all morphological structures, it is a cop-out to relegate all unexplainable phenomena as arising from unique historical events.

Hierarchy and evolutionary analysis. We need a context within which to study macroevolution. J. W. Valentine (1968, 1969) first suggested to paleontologists that large-scale evolutionary studies should use a hierarchical framework (e.g., Allen and Starr 1982; Eldredge 1985; Gould 1982a; Salthe 1985; Vrba and Eldredge 1984; Vrba and Gould 1986).

I use *hierarchy* in the sense of a series of nested sets. Higher levels are therefore more inclusive. There are at least two main hierarchies that we must consider: organismic-taxonomic and ecological. The organismic-taxonomic hierarchy can be ordered as:

> {molecules→organelle→cell→tissue→organ→organism→population→species→monophyletic group}

A variant of this hierarchy would include the substitution of *gene→chromosome→organism}* at the lower end. The ecological hierarchy would include: *organism→population→community.* There is no necessary correspondence, however, between levels of the ecological and organismic-taxonomic hierarchies.

Hierarchies can be used either as an epistemological convenience or as a necessary ontological framework for evolutionary thought. Both approaches have been taken in the past, sometimes within the same hierarchy. The standard taxonomic hierarchy is used commonly as a means to examine rates of appearance and extinction. Although different taxonomic levels may change differently over time, such studies do not assign special significance to these levels, as opposed to another set of levels that might also be studied (e.g., studying species, subfamilies, and families, as opposed to species, families, and orders). They are just conveniences whose ascending order of ranking may correlate with differences of response (e.g., Valentine 1969). On the other hand, some regard certain taxonomic levels as fundamental and of ontological significance. Van Valen (1984) sees the family level as a possible unit of adaptation. The species has been claimed to have great importance (Eldredge and Gould 1972). I and most neo-Darwinians see the organism as a fundamental level of the hierarchy, around which all other processes turn. If a given taxonomic level has meaning, it is because the traits of an organism can be traced to this taxonomic level.

If all processes could be studied exclusively with the smallest units of the hierarchy, then two conclusions would readily follow. First, it would not be necessary to study higher levels (i.e., there would be no macroscopic principles). Second, higher levels would be simple sums of the lower ones, with no unique characteristics of their own. The first principle might lead a geneticist to claim that once genes are understood, the entire evolutionary process could be visualized as gene–environment interactions, with no consideration of the properties of cells, organisms, species, or monophyletic groups. The second might lead a paleontologist to argue that patterns of ordinal standing diversity are a direct reflection of species diversity (e.g., Sepkoski 1978).

Taking the hierarchy as given, we can ask the following questions:

1. Can one learn about the higher levels from the lower?
2. Can one understand processes at a given level without resorting to knowledge of other levels?
3. Is there any principle of interaction among levels, such as unidirectional effects exerted by lower levels on higher levels (e.g., those of genes on individual survival) but not the reverse (the effect of survival of individual organisms on the future presence of the gene)?

The first question raises the issue of *reductionism,* a major area of controversy in biology (e.g., Ayala and Dobzhansky 1974; Dawkins 1983; Lewontin 1970; papers in Sober 1984a; Vrba and Eldredge 1984; G. C. Williams 1966, 1985; Wimsatt 1980). It is a common belief that all aspects of biological organization can be explained if the entire genome were sequenced and all the nature and sequence of all proteins were known. In parallel with this argument, several biologists have proposed the gene as the unit of selection and the primary target of understanding. A theory at the level of the gene would then be extrapolated to a theory of the entire genome. In one case (G. C. Williams 1966), the claim was a healthy antidote to the proposal that certain forms of evolution can be explained only at another level of the hierarchy, the population (e.g., Wynne-Edwards 1962).

Although reductionism is often an object of scorn among evolutionary biologists (Wimsatt 1980, Gould 1982b), there seems to be much confusion about definitions. At least three concepts are often freely intermixed. First, reductionism may imply a *reducing science,* which can explain all phenomena in terms of a set of basic laws and units. In this conception of reductionism, biological constructs such as species, cells, and amino acids could be described completely in terms of the language and laws of physics. In evolutionary biology, the language and processes of Mendelian genetics might be substituted by the language and processes of molecular biology (Schaffner 1984). Second, reductionism is often used to imply *atomism,* where all phenomena of a science can be described effectively by laws involving the smallest ontological units. Thus, one might claim that the extinction of the dinosaurs could be explained with knowledge of their nucleotide sequences only. This is the type of reductionism often under attack by macroevolutionists (e.g., Gould 1983b; Vrba and Eldredge 1984). Some (e.g., Wimsatt 1980) attack reductionism as an *impractical attempt to explain phenomena in terms of the smallest ontological units of a science*. This does not imply that it is impossible to do so, only that it is so difficult that higher constructs of a hierarchy are more practical (Nagel 1961). This argument can also be made when, for adequate description of another science the use of a reduced science requires a myriad of complexities in language (e.g., translating Mendelian genetics into molecular genetics [Hull 1974]).

The confusion of these types of reductionism makes debate quite difficult. For example, geneticist Richard Goldschmidt was a reductionist of the reducing science kind (G. E. Allen 1974), even if he is remembered for immortalizing the distinct break of the species level. He believed that chromosomal effects could be reduced to physical laws. Yet, Vrba and Eldredge (1984) placed him on the side of holism. As another example, Wimsatt (1980) criticized the reductionist program, but only because it is impractical to explain many phenomena. From this argument alone, it would not be clear that he would reject the other two types of reductionism, if his objections to workability could be addressed. On the other hand, others find that certain levels have emergent properties, which are irreducible to lower levels of a hierarchy. This opinion, presumably, would also apply if a reducing science were available. In other words, if physics could subsume all biological processes, such individuals would criticize physics if it were atomistic. The attraction of both atomistic and reducing-science reductionism rests in their sweeping approach at explanation. If all scientific explanation could be accomplished with some minimal-level constructs in a single science, then we could achieve an essentially universal language. Keats decried Newton for reducing the poetic elegance of the rainbow to its vulgar prismatic colors. If, however, such a reduction were possible, then grouping concepts such as the rainbow would be superfluous. But can we find such basic elements and a set of relationary laws in science? Do we find emergent properties in higher hierarchical levels that cannot be defined in a language derived from the lower levels?

The dream of reductionism has never been achieved, nor does it seem likely that we will explain all by resorting to explanations using only the basic elements (Popper 1974). As we study different geometries, we learn that the detail lost in switching from Euclidean geometry to topology is superseded by whole new concepts that were never previously visible (Medawar 1974). In Euclidean geometry, shape is invariant and transformations and comparisons are based on angles, numbers of sides, and curvature about foci; topology ignores exact shape but maintains a sense of space and linear order. The transition from the former geometry to the latter involves a restriction of detail, but new concepts emerge. Thus, the notion of conic sections appears in the geometry of projection.

In evolutionary biology, the gene is often employed as the smallest unit of consideration, though recent discoveries of molecular genetics muddle this a bit.

Population genetics usually sees the fate of genes in terms of their contributions to fitness and stochastic processes. Complexities of genetic structure, such as epistasis and linkage, greatly complicate population genetic models. Yet it is a legitimate pursuit to ask how genes survive by virtue of their effects on the phenotype, although one might question the power of both our empirical tools and multilocus models to realistically attack population genetic problems (e.g., Lewontin 1974).

Most evolutionary biologists acknowledge a great deal of complexity in the effects of single genes on the phenotype and emphasize the complex interactions among genes. Most adhere to the principle that the organism, and not the gene, is the unit of selection (e.g., Dobzhansky 1970). The integrity of the organism and its internal interactions have been emphasized by Dobzhansky (1951), Lerner (1954), and Stebbins (1974), among others. Consider Stebbins's statement (1974, p. 302) of the limited evolutionary potential of the incorporation of new alleles:

> Mutations that affect these structures and processes have an adaptive value not in direct connection with genotype–environment interactions, but through their interactions with other genes that contribute to the structures or processes involved. In higher organisms, the majority of genes contribute in one way or another to these conserved structures and processes. The adaptive value, and hence the acceptance or rejection by natural selection of most new mutations, depends not upon direct interactions between these mutations and the external environment, but upon their interaction with other genes, and their contribution to the adaptedness of the whole organism.

This is not an appeal to mysticism. Stebbins merely acknowledged that genes serve to determine a functioning phenotype in a complex manner. Genes may very well be retained by virtue of their contributions to fitness, but there is an important hierarchical level, the organism, that also shapes the fabric of genetic organization. The organism is not the simple sum of its parts. It may well be that division of labor in some Hymenoptera serves the purpose of the survival of genes, but the phenomenon of labor division cannot be explained from the genes' mere presence.

The notion of levels is well entrenched within evolutionary biology, but the exact awareness of levels is not always present when evolutionary hypotheses are formulated. The effects of individual genes on fitness can be overshadowed by other processes, which are best considered as interactions of higher levels of the hierarchy with lower levels. Consider the many studies of regional gene frequency clines discovered by students of allozyme polymorphisms over the past few decades. Typically, one samples over a geographic–environmental gradient and finds a spatially progressive change in allele frequency at a locus (e.g., *Adh* for *Drosophila*). The distribution and abundance of the variant alleles have been studied by those interested in the question of natural selection. There is almost universal agreement that if the functional differences among allozymes could be related to fitness, then the problem of geographic variation would be solved. But is this true?

Effects within an evolutionary hierarchical system can be transmitted downward (Campbell 1974). For example, consider a step cline that transects a continent, with allele *a* nearly fixed in the east whereas *b* is fixed in the west. Suppose that a dramatic change in structural habitat (e.g., loss of the species' requisite food plant) drives to extinction the entire western part of the species. Owing to stochastic loss, the small remaining presence of allele *b* in the east fades out. The loss of the allele has nothing to do with effects of the locus on fitness; it is simply a consequence of selection at a higher level of hierarchical organization, the population. In all cases in which geography plays a role in genetic differences in a species, the difference between single gene selection and group selection can be similarly ambiguous (Levins 1970).

The question of considering levels of the hierarchy without resorting to explanations at other levels is of equal importance in evolutionary investigations. This can be as much a practical issue as a philosophical one. In an empirical study of diversity in the fossil record, for example, higher taxonomic levels may be more tractable than lower ones. Valentine (1968) was a pioneer among paleontologists in considering hierarchies from a paleoecological point of view. If hierarchies are "nearly decomposable" (Simon 1962), different taxonomic levels might respond variously to the same environmental processes. But if higher-level constructs are mere aggregates, one might study the abundance of taxonomic families over geological time without needing to count species.

But the response of families to aspects of earth history differ from the response of species. Families are, of course, constructs of species and therefore may have responses that can be predicted from the aggregated species of each family. The family level might, however, correspond ecologically to adaptive zones and therefore have its own unique response (e.g., Simpson 1953, Van Valen 1984). It is crucial in any hierarchical analysis of a system to understand (1) to what degree it is decomposable and (2) if the hierarchy is decomposable, the nature of the differences of response of different hierarchical levels to different processes.

Consider, for example the pattern of first appearances of phyla versus those of families (Valentine 1968). Phyla show a distinct peak in the rate of first appearances early in the Phanerozoic. Families appear and disappear continuously throughout the Phanerozoic. One might argue that phyla represent major turning points in the history of life: As a response to a series of open environments, developments of major evolutionary consequence came first. By contrast, family-level divisions may represent minor evolutionary changes that came and went in response to minor changes in earth and biotic history. Certain measures will have entirely different meanings at different levels of the hierarchy. The measure of individual productivity is fecundity; at the species level, however, speciation rate would be the appropriate measure. *Fecundity* and *speciation* have entirely different meanings, because speciation decouples two entities from further reproductive connection, whereas an organism's offspring would still be part of the same interfertile population unit. *Extinction* also has different meanings. At the organismal level, death does not necessarily entail the loss of given genes from the population; in the case of species extinction, it almost invariably does. At the level of the monophyletic group, entire character complexes will be lost.

Although generalizations about the interactions within hierarchies are difficult to make, certain evolutionary hypotheses are phrased most profitably in terms of a regularity of interaction within a hierarchical framework. Riedl (1978) argued, for example, that an ordering principle of evolution is "burden," which is the effect on the whole organism of a given evolutionary change. He argued that natural selection is a confrontation between the external aspects of the environment with the internal interactions of the organism. Evolution emerges from the continuing interaction between internal organismal organization and the effects of the external environment (Schmalhausen 1949). As such, the nature of internal order (we will not define this precisely for the moment) at a given time in a taxon's history is part of the measure of response to selection. This leads to the following hypothesis. With the evolution of increasing internal order, the functional burden, encumbered by any given response to natural selection, increases and "with this a new lack of freedom called canalization also increases" (Riedl 1978, p. 80). In hierarchical terms, Riedl (1978) argued that as the evolution of increasing internal order (presumably of development) proceeds, any new effect of selection on any part of the system (e.g., gene) will have increasing effects on the entire system (e.g., developing embryo). Thus, he predicted that the tightness of effect from the lower to the upper part of the organismal hierarchy will increase with evolutionary time.

Jacob (1977) has proposed a related hypothesis, based on a presumed hierarchical structure of organization within the living organism. "Highly evolved" organisms are not perfectly evolved machines at all. Rather, the process of evolution acts in the way that an engineer tinkers with an invention while "improving" it. This leads to machines and organisms that have a peculiar set of internal constraints that can be explained only by history. As Darwin (1859) recognized, the process of evolution via natural selection should build up complex and imperfect organisms with limited abilities to deal with environmental change. "Nor ought we to marvel if all the contrivances in nature be not, as far as we can judge, absolutely perfect. The wonder indeed is, on the theory of natural selection, that more cases of the want of absolute perfection have not been observed" (Darwin 1859, p. 472).

Hierarchies are thus the natural framework for the study of the evolutionary process. Having the wrong gene could conceivably extinguish a phylum. Extinguishing a phylum could, by accident, extinguish a gene. The hierarchical approach allows the organization of research programs to tackle such questions that are historical in nature.

In the context of hierarchies, the macroevolutionist critique of Modern Synthesis rests in the belief that selection at the level of organism and levels beneath is inadequate to explain the entirety of evolution. This is predicated on the belief that processes relating to larger groups can result in evolutionary change. The principal example of such a process is the balance of speciation and extinction, which might produce biased morphological change (Eldredge and Gould 1972, Stanley 1975). This claim is not at odds with the presence of selection at lower levels of the hierarchy. Rather, it suggests an expansion of possibilities in the explanation of evolutionary trends. At the least, one can argue intuitively that extinction strongly affects the relative proportion of taxa and, therefore, the spectrum of morphologies. Because habitat destruction is often a major source of extinction, it is not very controversial to claim that extinction would not be tightly linked to individual genes in many cases. What would be controversial is to argue that such processes caused the evolution of complex morphological structures such as the cephalopod eye. Here, neo-

Darwinians would stand firm in ascribing such an evolutionary process to natural selection working on the interactions of genes and the organism.

The Role of Type in Evolutionary Concepts

Typology and evolution. The problem of macroevolution has always been regarded as the problem of the origin and evolution of types and the present gulf between them. A type is a class whose members share a certain set of defining traits. Such a definition implies gaps between types, or at least discrete differences in the sets of traits that define the different types. If you don't believe in types and gaps, then you don't worry much about major evolutionary jumps, but the belief in types, among species or among higher taxonomic constructs (e.g., baupläne) will lead you toward a deep concern about discontinuities in evolution.

We should distinguish among three sorts of typologies that permeate the study of biology:

- *Essentialist type or idealistic type:* The type has a fixed immutable essence. Minor variation is possible within the type.
- *Modality descriptor:* The type is of a modal form, defined by the overall properties of a population. Intermediate stages between the types are possible but uncommon, at least at present.
- *Saltatory type:* The type has a fixed set of properties, but it is changeable into other discrete types only via a saltatory process. Intermediate stages would be claimed not to exist or to ever have existed.

The deep-seated belief in types derives from an *essentialist* philosophy, which views the world as a series of entities defined by their respective essences. The ordering of these entities is usually associated with a teleological view of the universe. In the biological context, species are viewed as constant and immutable. Aristotle thought of natural selection but dismissed it in favor of a world of teleology and types. Certainly the deep-seated belief in essentialism, commonly held by as disparate a set of intellectual luminaries as Aristotle, Bacon, Mill, and Cuvier, would have tended to freeze all scientific notions of the potential mutability of species (see Hull 1973). To Cuvier, for example, species were perfectly adapted to a specific environment. If the environment were eliminated or altered over time, the immutability of the species would ensure its extinction, making transitional changes inconceivable.

The problem of the biological concept of type gains modern relevance through the theory of evolution, particularly that espoused in Darwin's *On the Origin of Species by Means of Natural Selection* (1859). The pre-Darwinian notion of the perfection of design being a manifestation of the work of God accepted the types as perfectly adapted designs. It is in the post-Darwinian morass of species mutability that the essentialist notion of types takes on a nonscientific connotation. Perfection and perfect adaptedness gave way to the "law of the higgledy piggledy," as Herschel called it. Organisms were often out of step with their environment and natural selection culled out less well adapted variants. Successive forms were not necessarily perfect, according to Darwin; they only happened to be the fittest of the lot.

Aside from a decidedly nonteleological abandonment of perfection, Darwin's theory concluded that species were mutable. Darwin's conception of evolution presumed that every pair of ancestral and descendant forms comprised the end towers of a bridge of a (not necessarily evenly) graded series of intermediates spanning the chasm. Gaps between successional fossil forms could be explained by two possible shortcomings of the data of paleontology: (1) the new species arose via a string of intermediates in a small and isolated population not preserved in the fossil record and (2) the series of intermediates could not be preserved owing to frequent gaps in the fossil record. If only the gaps could be filled, then we would find our intermediates. Was Darwin right? We will discuss this issue in chapter 6. Whether right or wrong, Darwin clearly was antitypological.

The transitional period between the dominance by typological idealists such as English morphologist Richard Owen and the new generation of evolutionists led by Darwin and Huxley was a bit more muddled than is generally realized (see discussions in Desmond 1982; Ospovat 1981). Although Owen vigorously opposed the godless role of chance and the purposeless force of natural selection, he nevertheless came to believe in extensive gradual change from a primitive ancestor, all within a general archetype. The archetype, however, contained an essence that was to be revealed among the members by the study of homology. Thus, he saw vertebrate evolution as a gradual process and even managed to find a transitional form, *Archegosaurus,* that obliterated the gap between reptiles and fish. Owen's (1859) reconstruction of the evolution of the Vertebrata even included a concept of branching and was therefore decidedly close in spirit to Darwin's (1859) hypothetical phylogeny diagram and Haeckel's later attempts at phylogenizing in the *Generelle Morphologie* (Bowler 1976).

By contrast, Thomas Huxley, "Darwin's bulldog," held at first to a typological view of species that probably derived from his adherence to Charles Lyell's concept of nonprogression in evolution (Desmond 1982, p. 90). This viewpoint led him to believe, despite evidence to the contrary, in the early Paleozoic origin of mammals, and in *persistence,* a concept that allowed no major progressive evolutionary trends. This latter belief was in conflict with that of Darwin, his idol, who said "I cannot help hoping that you are not quite as right as you seem to be" (quote in Desmond 1982, p. 86). In this context, Huxley's prepublication warning that Darwin's *Origin* was too enthusiastically against saltation seems more derived from confusion and mixed loyalties than prescience. In a way, Huxley's belief in persistence was more inimical to the establishment of evolutionary trends with empirical evidence than was Owen's idealized archetype, within which some evolutionary change was accepted.

An association of phyletic gradualism with nineteenth-century liberalism (Eldredge and Tattersall 1982; Gould and Eldredge 1977) is an oversimplification. One associates a belief in slow progress with this period in history. But Darwin was not part of the mob: He eschewed the notion that evolution was to be understood as progress toward higher forms. Darwin's belief in slow evolution may indeed have derived from the Victorian belief in slow progress, but the notion of continuous gradational transformation was held in many non-Darwinian quarters in the mid-nineteenth century. Owen strongly believed in phyletic gradualism and was clearly associated with the forces of privilege and station. It apparently served his purpose to believe in evolutionary radiation, however, because it weakened the position of the followers of Lamarck (Desmond 1982, p. 69). His notion of transmutation had limits, and they were those that fit safely within a theistic philosophy. Darwin's conception of nature, red in tooth and claw, was, if anything, repugnant to the Victorian zeitgeist.

Huxley spoke clearly for the new emerging class of individuals whose station was to be recognized by their own efforts. Yet, until the late 1860s, he stood intransigently opposed to evolutionary progress while, at the same time, he fought vigorously for the working class and worked actively to help install a new generation of meritocratic professionals. As Ospovat (1981) wisely noted, the notion of phyletic evolution, with an inferred directional series of gradational forms, would have developed even if Darwin's *Origin* had never been published! The notion of gradualism came from the morphological tradition and did not originate with Darwin. Think of Lamarck, whose notion of gradual change and inevitable evolutionary directionality through acquired inheritance might have been the accepted paradigm of evolution had Darwin and Wallace not come along. As Riedl (1978) noted, even Goethe's philosophy, so clearly typological, allowed for extensive variation within the type (see also Sherrington 1949).

Essentialism ends with the rise of population thinking. The history of progress of twentieth-century biology can be broken down into four discrete periods. The terms I use to describe them are used disparately.

Mutationist–biometrician debate. The mutationist-versus-biometrician period covers the first two decades of the twentieth century, contemporary with the rediscovery of Mendelian variation and the early investigation of chromosomes. Two schools of thought were popular. The *biometricians,* led by such luminaries as Pearson, Galton, and Weldon, had by this time developed a battery of statistical techniques to analyze natural variation in populations. In contrast, the rediscovery of Mendelian transmission inspired another school of thought, led by deVries, Bateson, and Morgan (at first), to emphasize the discontinuous mutations found in laboratory experiments. This school saw *mutationism* as the stuff of evolution and rejected natural selection on existing variation (Bateson 1894). The belief in quantum jumps from one type to the next by mutation versus a belief in natural selection on continuous variation was a false dichotomy. The controversy hampered the growth of population genetics for a decade (see Huxley 1940; Provine 1971). The belief in steplike differences between types (mutations) froze our outlook on natural variation. We now appreciate that mutations occur at all levels of variation and that their presence in steplike transitions is far from being incompatible with the theory of natural selection. Mutation is understood as the source of variation on which natural selection can act.

Neo-Darwinian period. Covering the approximate interval 1920 through 1937, the neo-Darwinian period was marked by the survival from the past century of a host of now-defunct hypotheses such as Lamarckism and orthogenesis. But, most importantly, Sewall Wright, J. B. S. Haldane, and R. A. Fisher laid the foundations for genetic analysis of traits and genetic changes in populations. The power of natural selection was discovered, starting from an initial report by Punnett (1915), and a debate arose about the relative importance of stochastic versus deterministic effects in population genetics. All three of the neo-Darwinian triumvirate, however, seem to have believed firmly in the preeminence of natural selection (Mayr 1982a; Provine 1983). A series of intense debates on the role of drift in small populations were extremely important in focusing attention on several empirical systems, such as *Panaxia* and *Cepaea* (Provine 1983).

Modern synthesis. The Modern Synthesis period starts with the publication of Theodosius Dobzhansky's seminal work *Genetics and the Origin of Species* and culminates with the famous conference at Princeton University in 1947 (see Jepsen, Mayr, and Simpson 1949). The theoretical advances made during the neo-Darwinian movement were incorporated into systematics, ecology, and, to a degree, paleontology. Older concepts lingering in evolutionary biology, such as orthogenesis and Lamarckism, were discarded. Along with Dobzhansky, Ernst Mayr, Bernhard Rensch, George Gaylord Simpson, and Ledyard Stebbins were crucial contributors. The period was marked by a harmony never seen before or since. Of course, the neo-Darwinians were still actively contributing to evolutionary theory, and Sewall Wright contributed to the Princeton conference. Ernst Mayr (1982a) has argued that they did not influence the Modern Synthesis, but both Dobzhansky's (1937) and Simpson's (1944) texts show strong influence from theoretical population genetics (e.g., Provine 1983; Laporte 1983).

From the beginning of this period, all architects of the Modern Synthesis followed their neo-Darwinian forebears in believing in the primacy of natural selection in shaping evolution. A few nagging examples of claimed random variation – for example, inversion polymorphisms in *Drosophila* – turned out to be strongly selected (e.g., Dobzhansky 1948a, 1948b). This only strengthened the general feeling for the importance of natural selection. Gould (1983a) argued for a "hardening of the Modern Synthesis" and suggested that factors other than natural selection were actively suppressed. As the founders of the neo-Darwinian movement and its architects all believed in the primacy of natural selection from the beginning, it seems contradictory to conclude that any "hardening" could have taken place (Levinton 1984). Gould saw the 1930s as a time of pluralism; if orthogenesis and Lamarckism were what he had in mind, we could have lived without this pluralism. The further move of the Modern Synthesis toward population thinking and experimental approaches was the healthiest episode in the twentieth-century history of evolutionary biology.

Postsynthesis period. As in any historical period following a major congealing, the postsynthesis period is marked by disarray. At first, the Synthesis came to dominate natural history. But two movements have directed current trends in the study of evolution. Wynne-Edwards's claim (1962) that group behaviors arise from group selection became a major concern. G. C. Williams's (1966) attack on this overall hypothesis attempted to restore the primacy of individual selection and an orientation toward the study of genic level natural selection. This response was contemporary with W. D. Hamilton's explanation of altruism in terms of benefit to the individual and was followed by the sociobiology movement (e.g., E. O. Wilson 1975), which has been the source of intense debate and criticism (Segerstråle 2000). Following the elucidation of the gene-protein specification process, a large degree of genic protein polymorphism was discovered (Harris 1966; Hubby and Lewontin 1966; Lewontin and Hubby 1966). This was surprising to the majority, who, from predictions of theory and experience with laboratory variation, saw gene loci in natural populations as relatively invariant, with rare mutants of low fitness. From this came the neutral theory of evolution, the first credible theory that incorporated stochastic processes to explain variation in living systems (see Kimura 1983). Of course, many selectionist explanations for molecular variation have been tendered as well (see chapter 3), but the issue has not yet been resolved. Newer methods have allowed the investigation of selection at the level of DNA sequences.

The Modern Synthesis, a period during which genetics, systematics, and population genetic theory blended into a supposedly harmonious neo-Darwinian view of evolution (Mayr and Provine 1980), was also a time when typological thinking was under attack. Mayr (1942), in particular, was a great pioneer in exposing the traditional methodologies of systematists as basically typological. He wrote:

> The taxonomist is an orderly person whose task it is to assign every specimen to a definite category (or museum drawer!). This necessary process of pigeon-holing has led to the erroneous belief among nontaxonomists that subspecies are clear-cut units that can be easily separated from one another. [Mayr 1942, p. 106]

and:

> The species has a different significance to the systematist and to the student of evolution. To the systematist it is a practical device designed to reduce the almost endless variety of living beings to a comprehensible system. The species is, to him, merely one member of a hierarchy of systematic categories. [Mayr 1942, p. 113]

Even Darwin, although believing that at least some species were in the process of changing and that certainly all species were mutable, held a rather practical view of delineating species:

> In determining whether a form should be ranked a species or variety, the opinion of naturalists having sound judgement and wide experience seems the only guide to follow. [Darwin 1859, p. 47]

These quotes reflect a traditional reliance of systematists on the presence of types. But it is not always clear whether this reliance stems from essentialism or from a practical attempt to classify the world's creatures. It is doubtful that twentieth-century systematists adhered to an essentialist concept of species. More likely, they incorporated some intuitive notion of statistical recognition among modes between more continuous morphological gradation. In the period preceding the Modern Synthesis, most systematists saw species as distinct and definable by characteristic differences that arose by some sort of nonadaptive process (see Gould 1983a; Provine 1983).

The Modern Synthesis substituted a new concept of species for older concepts. The modern biological species concept (Dobzhansky 1935) defined speciation as a stage in a process "at which the once actually or potentially interbreeding array of forms becomes segregated into two or more separated arrays which are physiologically incapable of interbreeding." Although this concept has been modified and redefined in terms of the fitness of hybrids versus that of intrapopulation crosses, the basic concept has survived and is still widely regarded as a natural definition of species, although the suggested mechanisms of species formation are varied (see chapter 3).

The new definition of *species* has carried with it a more sophisticated concept of type, based on a process that produces modality of form rather than on an inherent and undefinable essence or the expectation of saltation. The biological mechanism of reproductive isolation ensures the possibility that the forms of two daughter species can go their separate ways. It acknowledges a materialistic basis behind the ability of both native peoples and systematists to arrive at nearly the same species divisions. As Dobzhansky claimed:

> ...the living world is not a single array of organisms in which any two variants are connected by an unbroken series of intergrades, but an array of more or less distinctly separate arrays, intermediates between which are absent or at least rare. [Dobzhansky 1937, p. 4]

Dobzhansky's notion of type as modality is committed to the mechanism of speciation through reproductive isolation and certainly eschews the notion of essence. A well-known critique of the reality of the biological species concept (Sokal and Crovello 1970) also avoids the issue of essentialism; it simply attempts to criticize the utility of the Dobzhansky–Mayr biological species concept to practicing systematists and claims the importance of phenetic similarity in systematic work. Typology as essentialism is properly absent from their arguments.

Both Ghiselin (1975) and Hull (1976, 1980) argued that if species are to be treated as classes (e.g., *Homo sapiens*) with a set of members (e.g., Martin Luther), then the class becomes effectively immutable and just as essentialist as pre-Darwinian notions of species or higher taxa. Hull (1976) recommended that a species be regarded as an entity with spatial-temporal and genetic continuity. As such, it effectively became an individual, bearing a proper name – that is, the specific name. The border between one species and another under this approach could be arbitrary, although Hull accepted that mechanisms such as Mayr's (1963) theory of speciation might tend to sharpen the borders between species. This individualistic concept is therefore not essentialist.

The old essentialist notions of type still pervade our thinking. The typological approach, transformed into an evolutionary guise through the late nineteenth century by great morphologists such as Gegenbaur, initiated a research program that accepted the concept of evolution yet stuck closely to an idealistic system. Coleman (1976) noted (p. 172), "Seemingly new organisms could always continue to appear [via evolution] in the world of objective reality, but the idealistically inclined morphologist claimed the power to discern the unvarying form or forms to which these appearances properly belonged." Thus, although evolution was taken to be the grand justification for the study of comparative morphology, a residual belief in typology prevented a study of variation and focused study on homology, with no consideration of process. This led the field of comparative morphology toward academic disaster in the twentieth century and prevented advancement relative to nonessentialist-dominated fields such as population genetics and molecular biology (Coleman 1976). This does not mean, however, that baupläne do not exist – only that a subtle essentialism has inhibited our capacity to study their possible materialistic basis.

An appropriate point of departure for the study of transitions in evolution was succinctly outlined by Dobzhansky. Two groups of organisms in two-dimensional space have a gap between them. Did one give rise to the other? If so, then why is the gap present? Is it hard to traverse? What is the pathway of the traverse? How fast was the change effected? These questions arise and can be approached objectively only when the mutability of the "types" is admitted and evolutionary relationships can be determined. Characters and their mapping on cladograms are the key to avoiding types.

The mind-set of typology is not limited to arguments over taxonomic categories. Even the functional morphologist can be led to types, with intervening gaps where no intermediate is to be found. D'Arcy Wentworth Thompson revealed his prejudice in the following passage from his *On Growth and Form*:

> A "principle of discontinuity," then, is inherent in all our classifications, whether mathematical, physical, or biological, and the infinitude of possible forms, always limited, may be further reduced and discontinuity further revealed. . . . The lines of the spectrum, the size families of crystals, Dalton's atomic law, the chemical elements themselves, all illustrate this principle of discontinuity. In short nature proceeds "from one type to another" among organic as well as inorganic forms; and these types vary according to their own parameters, and are defined by physical-mathematical conditions of possibility. In natural history Cuvier's "types" may not be perfectly chosen nor numerous enough, but "types" they are; and to seek for stepping stones across the gaps is to seek in vain, for ever. [Thompson 1952, p. 1094]

In the passages preceding this quotation, D'Arcy Thompson argued that the nature of growth and function had most probably erased much of the vestiges of morphology that might be used to reconstruct phylogeny. Thompson's views are reminiscent of those of the anti-Darwinian Mivart (1871), who also likened the differences among forms to the laws of crystallization. His typology is clearly quite different from that of the essentialists and quintessentially the opposite of Gegenbaur's. He believed, nevertheless, in some mechanism or axiomatic condition that underlies a typological system. Are the stepping-stones never to be found?

Macroevolution and the Fall of Goldschmidt

Hopeful monsters and hopeless mooting. Studies of macroevolution tend to either idolize or denigrate the role of the geneticist Richard Goldschmidt. I find myself in between the extremes. He is best remembered for *hopeful monsters* (Goldschmidt 1933, 1940), those few monstrosities that he claimed to be the stuff of major species-level saltations in evolution. He relied on hypothetical chromosomal mutations that accumulated cryptically in populations until a threshold was breached, propelling the phenotype across an unbridgeable gap. Most of these new phenotypes were hopeless, but the rare success was the progenitor of a new species. This work has not withstood the test of time and was at variance with the fact and theory contemporary with its proposal and all that we have learned since. But Goldschmidt's work includes a more visionary thread attempting to integrate genetics, development, and evolution, which was largely ignored until the 1990s, despite other standard-bearers for the approach (e.g., Waddington 1957, 1962).

After a long and successful career, Goldschmidt – a Jew – was dismissed from his academic position in Berlin. After leaving Nazi Germany, Goldschmidt came to the United States and settled at the University of California, Berkeley. Among his important works in English are *Physiological Genetics* (1938) and *The Material Basis of Evolution* (1940). The latter brought him into disfavor with his contemporaries, so much so that he wrote a bitter reprise to start his 1945 (a, b) papers on the evolution of Batesian mimicry in butterflies.

Why was Goldschmidt so isolated from the pillars of the neo-Darwinian period and the Modern Synthesis? He proclaimed that "The neo-Darwinian theory of the geneticists is no longer tenable" (Goldschmidt 1940, p. 397). He argued that "there is no such category as incipient species. Species and the higher categories originate in single macroevolutionary steps as completely new genetic systems" (ibid., p. 396). The first part of the book, entitled "Microevolution," described the nature of geographic and within-population variations in a species. The second part denied that this was the stuff of transspecific evolution. His adherence to this strong point of view is exemplified in his endorsement of the contemporary work of the paleontologist Otto Schindewolf (1936), who had proclaimed that the first bird had hatched from a reptile's egg.

Both of Goldschmidt's books displayed a strong empirical approach to the nature of variation and the varied relationship between development and genetics. But his final prescription for solving the mystery of mysteries, as Herschel described the origin of species, was dogmatic and simplistic: saltation. Goldschmidt admired simplicity – "a simplistic attitude is not a flaw but the ideal goal for a theory in science" (Goldschmidt 1940, p. 399).

Despite the apparent simplicity, Goldschmidt's views were based on a false dichotomy between broader-scale chromosomal mutations and point mutations, which were presumed to be the neo-Darwinian basis for evolutionary change. Neo-Darwinians took variation for granted and made no strong distinction between single genes and larger genetic constructs, so long as they obeyed Mendelian rules. Goldschmidt's claims that neo-Darwinians believed solely that races were incipient species are also at variance with the many saltatory mechanisms of speciation that had been previously proposed (see Templeton 1982). In sum, Goldschmidt's characterizations of the neo-Darwinian movement were inaccurate caricatures.

Goldschmidt felt that the population geneticists of the day were too faithful to the notion that genes were independently acting entities. Some discoveries, such as the notion of position effects of genes, strengthened his suspicion of the genic theory. This feeling might have stemmed from his training, which emphasized development and physiological function, as opposed to transmission genetics (G. E. Allen 1974). His interests in physical science might have also given him the standard 1930s philosophical mistrust of theories that depended on the importance of fundamental units. His own theories of gene action required instead large-scale integrated effects of chromosomes. These theories were mainly metaphorical in nature and were shown to be untenable in subsequent decades.

Aside from the problems of Goldschmidt's mechanism of the rise of novelties, his ideas of spread and speciation also were not well received. The arguments against the spread of novel and extreme variants appearing only rarely had been well understood by then and have been subsequently amplified. Rare variants tend to become extinct very rapidly. Dramatically different mutations are most likely of low fitness relative to the population mean phenotype (Fisher 1930). Relative to extreme phenotypes, mutants of less extreme form are much more common and therefore contribute in greater proportion to a population's evolutionary potential (e.g., H. J. Muller 1949).

In commenting on Schindewolf's ideas, Mayr was confident that major saltations in evolution were nonexistent when he stated:

> No special evolutionary processes need to be postulated, even in groups where such missing links have not yet been found and where the primitive roots of the various stems always seem to be missing. [Mayr 1942, p. 297]

George Gaylord Simpson also was secure in his belief that transitional forms were common in evolution. He commented wryly:

> The argument from absence of transitional types boils down to the striking fact that such types are always lacking unless they have been found. [Simpson 1950, p. 233]

A specific controversy illustrates why Goldschmidt's ideas quickly lost favor, at least among neontologists. At the time Goldschmidt was writing his famous second book, *The Material Basis of Evolution,* Batesian mimicry in butterflies had already become the subject of genetic research. The now-famous Punnett (1915), a protégé of William Bateson, believed that the mimetic morph in species of the swallowtail butterfly genus *Papilio* could be explained by a single integrated genetic variant. Goldschmidt's (1945a) interpretation of mimicry in *Papilio* followed directly from his ideas on developmental regulation, genetic integration, and saltation. He argued that major switch genes explained the evolution of a mimic from a nonmimetic ancestor. Developmental constraints would cause the same mimetic phenotype, controlled by the corresponding genotype, to appear repeatedly in different species.

Goldschmidt was far off the mark. The work of Clarke and Shepard (1960a, 1960b, 1962, 1963) presented a detailed picture that was consistent with a hypothesis of gradual selective buildup of the mimetic phenotype and significant differences in the genetic mechanisms behind the evolution of the mimic within populations of the same species, let alone among species (see J. R. G. Turner 1977, 1981).

To illustrate, consider the case of *Papilio memnon,* a species widely distributed in Southeast Asia (Clarke, Shepard, and Thornton 1968). Populations of *P. memnon* vary from place to place and can be nonmimetic or strikingly similar to various local models. They have, however, consistently failed to evolve red markings on the body that are characteristic of the models. Clarke and coworkers found that several closely linked loci were major contributors to the buildup of the mimetic phenotype. Mimicry was found, as in other species of *Papilio* (Clarke and Shepard 1963), to be controlled by a so-called supergene (the closely linked loci), which had most probably evolved gradually by the accumulation of closely linked allelomorphs in advantageous combinations. The selective stability of such supergenes, once evolved, has been confirmed theoretically (Charlesworth and Charlesworth 1976). Two other unlinked genes were also involved in the construction of the phenotype. Note that, in this context, gradual does *not* refer to an infinitesimally fine series of morphs ranging from nonmimetic to mimetic. Some of the contributing genes do make rather major jumps "toward" the mimetic phenotype, but these certainly do not amount to the magnitude of change required by Goldschmidt. This is only one example demonstrating that the Modern Synthesis by no means commonly accepted only insensibly small changes in evolutionary transitions.

Most importantly, crosses among mimetic races illustrated the differences of local evolution among races. The resemblance of progeny of interracial crosses to either of the local models was found to be better in none of the crosses, approximately as good in 10, and poorer in 35 (Clarke et al. 1968). This refuted the notion that evolutionary outcome was constrained and involved identical genetic changes in all of the mimetic races. Also, modifiers affecting tail length, for example, were found to differ among populations.

Goldschmidt's Useful Developmental Approach

Although Goldschmidt is remembered for his saltationism, his books reveal a sophisticated notion of the nature of evolutionary novelty and potential for change. It is true that he held to an unduly strong version of the role of developmental constraint in evolutionary pathways. He also denied the value of experimental genetics in the study of transspecific evolution. These excesses should not conceal, however, his anticipation of the study of evolution via developmentally mediated regularities in the determination of form.

It is an unfortunate and inaccurate caricature of the neo-Darwinian and Modern Synthesis movements that adaptive evolution is infinitely powerful and is not constrained by forces other than the natural selection of optimal forms (as claimed by Gould 1980a). A substantial part of the literature of genetics and allometry acknowledges the constraints imposed by one set of traits on the evolution of others (see H. J. Muller 1949; discussion in Charlesworth, Lande, and Slatkin, 1982, pp. 476–480). Certainly Darwin was keenly aware that the evolutionary change of one trait was liable to bring about concomitant change in others, with no necessary concomitant adaptive significance (Darwin 1876, pp. 346–347), but an appreciation of this general problem falls short of Goldschmidt's profound understanding of the interrelationship of evolutionary direction and development. In recognition of this understanding, the volume by Raff and Kaufman (1983) on development and evolution was dedicated to Goldschmidt.

Consider the evolution of snakelike form in saurian lizards through the increase in vertebral numbers and rudimentation of extremities. Goldschmidt saw typical explanations as reflecting ignorance of the origin of pattern in development. Severtzov, for example, envisaged evolutionary change toward the fossorial habit as resulting from a series of steps, each involving a transformation of one caudal into a descendant sacral vertebra. The sacral vertebral column would be thus elongated and the position of the hind extremities shifted backward (cited in Goldschmidt 1938). Goldschmidt provided the following alternative explanation: "The evolutionary process changed primarily the basis of segmentation itself by altering its embryonic gradient and rhythm so that a larger number of segments was produced to begin with. The localization of the limb buds, and therewith the setting of the limits of thoracic and lumbar segments, is a deterministic process independent of the primary segmentation" (Goldschmidt 1940, p. 339). His explanation thus suggested an alternative developmental framework within which to view directionality in saurian evolution.

Physiological Genetics prescribed the general formula for the investigation of gene action. Goldschmidt not only appreciated the fact that genes often affected rate processes and that the phenotype was apparently broken up into a series of developmentally and probably genetically autonomous fields that were determined in a complex way as development proceeded but also actively applied these principles to his studies and interpretations of genetic variation and evolutionary potential. He attempted to popularize Spemann's notion of *determination stream*:

> We see that genes actually controlling color and structure of a wing may act by controlling a determination stream of definite quantity, speed of progress, pattern of flow, and action upon different processes of morphogenesis and chemism. [pp. 195–196]

Although the language seems archaic, the spirit of this approach is more vibrant than ever. Garcia-Bellido's (1975) important discovery of compartments in the development of *Drosophila* (see chapter 4) extended Goldschmidt's work on wing patterns in the gypsy moth, *Lymantria dispar.* Today, the "determination stream" has new life in the form of the study of conservatism in developmental gene action and in the role of epigenetic processes in organizing and constraining evolution. Unfortunately, we have lost Goldschmidt, who is usually not cited in works in this field (e.g., Alberch 1982; Bonner 1982; Gould 1982b; Maderson et al. 1982). Such is the power of the "hopeful monster" concept promulgated in Goldschmidt's disastrous second volume. It effectively erased the potential positive effect of his pioneering earlier work and probably abscised his potential ability to hasten the rise of a major research field integrating evolutionary and developmental biology. The tension between the followers of the Modern Synthesis and those of Goldschmidt's heterodox views clearly gave macroevolution a bad name and it became associated with major saltations between ancestor and descendant species. Thus, Goldschmidt contributed little to the arguments of the day other than a sterile counterpoint to the Modern Synthesis.

The German paleontological tradition also involved beliefs in heterodox notions such as orthogenesis and major saltations in evolution. Although Schindewolf's (1936) saltationism continued a German morphological-paleontological tradition (see Reif 1983a), it failed to elicit a following among English-speaking paleontologists and never led to a useful program of paleontological-evolutionary research in Germany. Thus, the German paleontological tradition also failed to penetrate evolutionary thinking in the English-speaking world. But the same period of the late 1930s and 1940s included another major movement in paleontology, pioneered largely by George Gaylord Simpson and later by Norman D. Newell (e.g., 1952), which made great progress in the understanding of evolutionary biology and macroevolution.

Macroevolution and Paleontology

Simpson's seminal role in rejuvenating paleontology. Simpson's pioneering volume *Tempo and Mode in Evolution* (1944) described, on the grand scale, variations in rate and qualitative changes in the history of life, as understood from the fossil record. With a brilliant and sweeping look at the history of life, he brought home three major points:

1. The ebb and flow of fossil forms and the temporal variation seen in morphological change and distribution patterns were both completely compatible with the then newly synthesized ideas of modern evolutionary biology.
2. Rates of morphological change had not been constant in the fossil record; periods of rapid change were often followed by periods of quiescence. The periods of rapid change were influenced strongly by ecological forces.
3. Rates of evolution differed widely among taxonomic groups.

This work and the later *Major Features of Evolution* provided paleontology with the means to awaken from its long-standing isolation from the popular twentieth-century movements in evolutionary biology. It also asserted a unity of purpose among natural historians. Alas, *Tempo and Mode* did not have immediate impact among paleontologists; it was hardly reviewed by paleontological journals, though neontologists welcomed it as at once an excellent and critical discussion of the theory of the neo-Darwinians and the provider of the important additional dimension of geological time (Laporte 1983).

Simpson's works made him the father of the "taxic approach" to paleontology, a field that employs changes in taxon richness and longevity to understand major patterns in the history of life (see chapter 7). This approach occupies a major part of the efforts of paleontologists today (e.g., Flessa and Imbrie 1973; Raup 1976a, 1976b; Sepkoski 1981, 1984, 1993; Valentine 1969; Van Valen 1973b, 1984). Simpson contrasted longevities within major taxonomic groups. The variations and general correlations of taxonomic longevity, speciation, and extinction rates have been used extensively to draw inferences about the tempo and mode of evolution (e.g., Sepkoski 1984; Stanley 1979), although many criticisms have been leveled concerning the potential of taxonomic bias generated by differences in morphological description, systematic practice, and so on, among taxonomic groups (e.g., Levinton and Simon 1980; Patterson and Smith 1987; Schopf, Raup, Gould, and Simberloff 1975; Van Valen 1973a).

Gould (1980b, p. 170) denigrated Simpson's work, relegating it to secondary thinking: "Simpson's synthesis unified paleontology, but at a high price indeed – at the price of admitting that no fundamental theory can arise from the study of major events and patterns in the history of life."

I find Simpson's contribution to be far more important. Simpson rightfully sought to establish a unification of basic principles between paleontology and neontology. This is only an admission that paleontological and neontological research must both acknowledge the premise that evolutionary principles operate similarly for extinct and recent biotas, though the specific circumstances might of course be radically different. Simpson believed from other evidence (e.g., Simpson 1952) that fluctuating rates of evolution in the vertebrates were due to the ecological conditions that might be observed today; but this stemmed from paleontological data, and not all paleontologists agreed (e.g., Newell 1952).

Paleontology had its own traditions that transcended the ability of Simpson or any other worker to alter significantly. Simpson did successfully debunk the notion of orthogenesis among North American paleontologists. But Simpson and the other founders of the Modern Synthesis failed to hasten a birth of activity on the part of paleontologists in documenting phyletic microevolutionary patterns. If this was Simpson's objective, then he failed rather miserably. As noted, his book was hardly noticed by paleontological reviewers. Indeed, until recently the "best" and most often cited quantitative paleontological studies of phyletic evolution dated no later than the 1930s (Brinkmann 1929; Rowe 1899). By contrast, Simpson's taxic approach, so quintessentially paleontological,[1] was followed and expanded later with great enthusiasm. To this very day, the taxic approach rules.

Paleontologists reconsider the fossil record and earth history. Perhaps the most important milestone marking the supposed integration of paleontology into the Modern Synthesis was the famous symposium for paleontologists and neontologists held at Princeton University in 1947 and published as *Genetics, Paleontology, and Evolution* (Jepsen et al. 1949). A series of papers published in that volume demonstrated the excitement of the time and revealed no major discord among paleontologists and neontologists, but the paleontological contributions were vastly larger in taxonomic level and time scale than were the neontological contributions. In a similar symposium in 1980 (Levinton and Futuyma 1982), my colleagues and I were struck by a maintenance of this difference of outlook. But the general uniformity of objectives in 1947 was by 1980 replaced by discord and a complex network of opposing camps (Futuyma, Lewontin, Mayer, Seger, and Stubblefield 1981; Lewin 1980; Schopf 1981; Templeton and Giddings 1981).

Another symposium organized by the Paleontological Society in 1949 (Woodring 1952) was a bellwether of a major direction of paleontological research that survived to the present. An attempt was made to relate environmental variations in the history of the earth to fluctuations in the origins of biotic groups and temporal

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[1] Simpson's taxonomic overturn approach probably derives from Charles Lyell (1831–1833), who used the rate of taxic overturn in the mollusks as a method to estimate the amount of geological section missing in the early Tertiary. He judged the mammals to have too rapid an overturn to be useful in this regard (Rudwick 1972). It is probably no accident that Simpson used the same two taxa in his *Tempo and Mode*. These were still, in the mid-twentieth century, the best and most accessible databases to paleontologists.

changes in taxonomic richness. An interesting conflict developed between those who found that temporal variation could be related to geological period boundaries, marine transgressions, and the like (Moore 1952; Newell 1952) and those who could find no such clear relationship (Cooper and Williams 1952; Simpson 1952). Simpson (p. 370) argued that "the evidence ... is consistent with the view that most of the broad features of vertebrate history might have been much the same if the earth's crust had been static." Newell, on the other hand, related bursts of evolutionary activity to rises in sea level. At the close of the symposium (Woodring 1952, p. 386), M. K. Elias questioned the entire data analyses of some of the contributors by claiming that paleontological collections were likely to be strongly correlated with sediments available for fossil sampling. This argument was to be repeated later (Raup 1976a, 1976b).

The attempt to establish a relationship between events in earth history and major patterns of abundance of fossil groups became a primary concern in the 1960s and 1970s. Changes in taxonomic richness were related to sea level changes (Newell 1952), sea-floor spreading (Valentine and Moores 1971), tectonism (Flessa and Imbrie 1973), stochastic processes (Raup, Gould, Schopf, and Simberloff 1973), ocean surface area (Schopf 1974), and asteroid impacts (Alvarez, Alvarez, Asaro, and Michel, 1980; Hildebrand et al. 1991), among other factors. A concern for the quality of paleontological data led David M. Raup and his colleagues to question the validity of taxon richness data (Raup 1976b) and to analyze temporal patterns in taxonomic diversity in a more meaningful way. Paleontologists became concerned with appearance–extinction patterns and some suggested that an equilibrium in diversity might be reached, though the various prescriptions and analyses differed considerably (Flessa and Levinton 1975; Levinton 1979; Rosenzweig 1975; Sepkoski 1984; Webb 1969).

It might be said that this movement only attempted to define the ecological theater and the grossest outlines of the evolutionary play. In some cases, however, important changes in the history of the earth were related to key evolutionary advancements. The advent of browsing organisms was, for example, related to the decline of worldwide blue-green algal mats in shallow water, a major environmental change (Stanley 1973b). Changes in the amount of oxygen in the atmosphere were related to the rise of eukaryotic organisms (Berkner and Marshall 1964; Cloud 1968) and the appearance of carbonate shells, which were effective in counteracting predation (Rhoads and Morse 1971). This approach has been revived in recent years, as studies of stable isotopes in ancient sedimentary rocks have suggested global swings in climate (Kaufman, Knoll, and Narbonne 1997).

This work distanced itself from studies of taxonomic diversity and adaptive radiation and the details of the evolutionary process at and below the species level. Most paleontological studies of evolution tended to outline the adaptive significance behind major radiations with little consideration for the detailed evolutionary processes behind morphological change. Trends at or below the species level were generally avoided and thought to be the "noise" that was to be filtered out in true evolutionary studies (e.g., Jeletzky 1955). Studies of functional morphology were usually extrapolated from studies of a single living or fossil species to broad evolutionary trends.

Paleontological focus at smaller evolutionary scales. Some important events and a few studies refocused the efforts of paleontologists on the details of the evolutionary process and led to the recognition among neontologists of the potential importance of paleontological data. The founding of the journal *Paleobiology,* the brainchild of T. J. M. Schopf, acknowledged that traditional paleontological journals had not broken away sufficiently from the old mold that allied paleontologists more to soft-rock geology than to evolutionary biology. As the issues of the journal were published (in 1975), those paleontologists concerned with areas of interest to neontologists suddenly appeared as a discrete group. This, in many ways, set the main backdrop for a strong effort by paleontologists to enter the center stage of evolutionary biology.

An article by Van Valen (1973a) analyzed the distribution of longevities of taxa of many disparate fossil groups and converted them into a series of log-linear survivorship curves. From this, Van Valen concluded that evolution was largely a result of the tangled bank of biotic interactions conceived by Darwin. His "Red Queen" hypothesis argued that random appearances of biological challenges regulated the tempo of evolution. This claim was of great interest to neontologists and was the subject of later speculation on the effect of random change on genetic load (Maynard Smith 1976) and diversity (Stenseth and Maynard Smith 1984). It also was an important link between the many studies of taxon longevity (e.g., Levinton 1974; Simpson 1944; Stanley 1975) at higher levels (generic and above) and processes occurring during speciation. To be blunt, the article led nowhere, really, and the relationship between taxonomic survivorship and the Red Queen was vague at best. This vagueness set a pattern in generating much debate that was more fostered by uncertain definitions than by substance.

A milestone in bringing a readjustment of paleontological focus toward the level of species and smaller-scale fossil trends was Niles Eldredge's (1971) attempt to refamiliarize paleontologists with the implications of then-current speciation theory for the study of patterns of morphological change in the fossil record, emphasizing the compatibility of Mayr's (1954, 1963) theory of peripheral isolates and genetic revolutions with observations of sudden change or gaps in the fossil record without transitional forms. Such gaps were also compatible with Darwin's (1859, p. 342) postulation of evolution in small populations in geographically restricted areas. Eldredge claimed that the neontological perspective made such gaps expectable. Ironically, the purpose of that article was to alert paleontologists that their ignorance of current evolutionary theory – that is, the body of theory stemming from the Modern Synthesis of the 1940s was actively hampering their ability to interpret data. Shaw (1969) claimed previously that paleontologists, in assuming that evolution occurred uniformly throughout a species range, were developing a highly inconsistent nomenclature at the species level. Eldredge's brand of the claim was later amplified and transformed, ironically, into the *punctuated equilibrium* hypothesis, a full-scale attack on the relevance of the Modern Synthesis to evolution (Eldredge and Gould 1972; Gould and Eldredge 1977, 1993; Stanley 1975, 1979).

Although the empirical aspects of the punctuative theory of evolution is discussed in detail in chapters 3 and 6, I will now discuss briefly its relevance to the recent history of evolutionary thought. The rapid origin of species, followed by a long period of stability, was posed (Eldredge and Gould 1972) as an alternative to so-called *phyletic gradualism,* which envisioned evolution as being even and slow and occurring by the transformation of an entire ancestral population into its modified descendants. Under the gradualism model, one could envision evolution as a stately, uniform, and slow progression from an ancestor to a descendant. Instead, the punctuated equilibrium theory saw evolution as a jerky process; speciation itself was rapid and the generator of morphological change. This model corresponded to Mayr's (1954) exposition of his peripatric model of speciation. Indeed, Mayr explicitly described the significance of the peripatric model in generating a fossil record filled with apparent saltations in evolution. After the speciation event, various constraints, including a centripetal force imposed by the homeostatic nature of development, tended to prevent change. The new species, deriving from a peripheral isolate, was equipped with "its own powerful homeostatic mechanism" (Eldredge and Gould 1972, p. 114).

Speciation was therefore the key event in evolution; evolutionary trends were to be envisioned as either variations in the rate of speciation (Vrba 1983) or selective deaths of daughter species in a biased morphological direction (Eldredge and Gould 1972; Gould and Eldredge 1977; Stanley 1975). This point of view led to a different perspective of evolutionary thinking. If speciation was a fundamental decoupling point in evolution, then major trends in evolution (i.e., macroevolution) should be thought of as "changes in species composition within a monophyletic group" (Eldredge and Cracraft 1980, p. 15). Phyletic evolution was not proscribed; it was simply a less important process.

The history of punctuated equilibrium is marked by furious debate, shifts in the definition of the concept, and self-congratulation (Gould and Eldredge 1993). At first, a strong definition asserted that speciation was the only time when morphological change occurred and stasis was the rule during the history of species. But at other times, Eldredge and Gould were content to argue that stasis – that is, a lack of morphological change over time – dominated the fossil record (Hoffman 1989a). The shifts in emphasis made it difficult to interpret what "tests" of the hypothesis really proved.

These arguments about the nature of the fossil record and claims about the adequacy of the Modern Synthesis nevertheless evinced a pronounced enthusiasm for the collection and analysis of paleontological lineages at successive horizons to search for gradual or punctuative patterns of morphological change. Gould and Eldredge (1977, 1993) managed to interpret most of the available evidence as favoring punctuations; others argued that the available database was inadequate or unsupportive of sweeping generalizations (Bookstein, Gingerich, and Kluge 1978; Sadler and Dingus 1982). Still others felt that the dichotomy between gradual and punctuative change obscured more than it clarified, because the pattern of morphological change does not uniquely imply a particular evolutionary process (summarized in Levinton 1983; Levinton and Simon 1980). Nevertheless, many causes célèbres were trotted out as paradigmatic examples of punctuation (e.g., Williamson 1981) or gradualism (Gingerich 1976; Malmgren and Kennett 1981; Sheldon 1987).

At the least, Eldredge and his colleagues generated a great deal of controversy and stimulated an examination of temporal change in the fossil record over smaller time scales.

In the 1990s, paleontological excitement shifted away from studies of diversity changes and microevolution, owing to a series of major discoveries that relate to the timing of the divergence of the animal phyla. Since the 1980s, the ranges of many animal groups have been extended to the Lower Cambrian (e.g., Jell 1980) and our understanding of the phylogeny of Cambrian groups has improved greatly (e.g., Smith 1988, 1992). But spectacular finds in the Lower Cambrian of China showed us that Burgess Shale–like fossils existed down to the base of the Paleozoic (Conway Morris 1989; Hou, Ramskøld, and Bergstrom 1991; Ramskøld and Xianguang 1991). The Burgess Shale, discovered by the great paleontologist C. D. Walcott (Yochelson 1996) was the most spectacular find of soft-bodied fossils in Cambrian rocks, but it left us with an intriguing range of enigmatic fossils, many of which were relegated to new phyla (Conway Morris 1985). The new discoveries pushed back the ranges of all fossilizable living phyla, and even some not expected ever to be preserved, to the Lower Cambrian (e.g., Chen, Dzik, Edgecombe, Ramskøld, and Zhou 1995; Shu et al. 1996).

The reinterpretations of the early history of life are coming so fast now that no volume will be current by the time it is published. The enigmatic nature of many of the fossils was used as a theme to argue that the Cambrian was a time of morphological and phylogenetic experimentation that never was to be repeated again in the Paleozoic. Gould's (1989) *Wonderful Life* argued that the fossils identified in Cambrian rocks were true oddballs – unique forms that deserved high taxonomic rank and that soon became extinct. Walcott was denigrated as failing to recognize that the Burgess Shale forms were often unique and instead took the conservative course and falsely allied his spectacular new zoo with living forms. Alas, *Wonderful Life* was dead on arrival at the bookstands, or at least on the critical list. Many of the seemingly weirdest forms had rather mundane connections to extant phyla, even including the wonderfully named *Hallucigenia,* whose unlikely orientation on long flexible spines was naively accepted for a time (Ramskøld and Xianguang 1991). The spectacular range of enigmatic Cambrian echinoderm fossils was explained as a fairly straightforward network of related forms that participated in a protracted evolutionary radiation (Smith 1988).

Although some of the mystery of Cambrian life evaporated, the suddenness of the apparent radiation of animal life was only accentuated by fossil discoveries and refinements of geochronometry. Cloud (1968) had argued that all so-called Precambrian fossils were bogus, and very few Precambrian animal fossils have been suggested since. This makes the appearance of the bulk of the animal phyla in the Cambrian an explosion. The famous Ediacaran fauna of Australia was Precambrian, but recent evidence suggests that this biota lived at least up to the beginning of the Cambrian and perhaps even into the earliest Cambrian (Grotzinger, Bowring, Saylor, and Kauffman 1995). Some have even suggested that the Ediacaran fauna is unrelated to the true Animalia (Buss and Seilacher 1984). Radiometric dating has bracketed the time over which the bulk of the animal fossils appeared, and the result is spectacular: the Cambrian Explosion of animal fossil appearances occurred over two Cambrian stages within about 10 million years! This has accentuated the wonder of the Cambrian Explosion, but naysayers have also appeared. Some question the uniqueness of appearance of the animal phyla in the Cambrian (Fortey, Briggs, and Wills 1996), whereas others have produced molecular evidence for a much deeper Precambrian divergence of the animal phyla (Wray, Levinton, and Shapiro 1996).

This story is now the central focus of studies in macroevolution. The discovery of new fossils, refinements of dating, characterizations of environmental change, and reinterpretations of animal relationships will all be part of the fabric of discovery and investigation for years to come. Paleontology is now concerned with origins and may have the tools to make substantial progress.

In this volume, I attempt to connect the threads of genetics, paleontology, and evolution to produce a framework for an integrated outlook on evolutionary theory and the fossil record. I try to evaluate the evidence and see just where paleontology and neontology can meet and make productive statements about the nature of evolution and the history of life. In some cases, my conclusions are optimistic; there is cause to believe that a new understanding of evolution is at hand. In other cases, the limitations of data and theory are apparent and we are still in the dark. Like Simpson, I am convinced that paleontologists and neontologists have something to say to each other and are capable of speaking a common language.

The Main Points

1. The process of macroevolution is the sum of those processes that explain the character–state transitions that diagnose evolutionary distances of significant taxonomic rank. The field of macroevolution emphasizes those processes that contribute to our knowledge of differences among major taxa but is not confined to evolution above the species level, or macromutations. Any process involved in the character transitions defined above is relevant to the field.
2. Biology and evolutionary thinking lends itself naturally to a hierarchical organization of the biosphere. The presence of distinct organizational levels begs the question of the reasons for their existence and the potential interactions among levels. Although we should eschew the assignment of undefined (mystical) properties to these levels, it is useful to understand whether some levels are particularly important in evolution. In cases such as extinction, elimination of higher levels (e.g., populations) may cause the elimination of lower-level units (e.g., genes). This is known as downward causation. In other cases, processes at lower levels (e.g., failure for a cold-adapting gene to be fixed in a population) might contribute to the loss of a higher level (extinction of the species, if the environment becomes cold). In some cases, such upward causation permits an interesting correspondence among levels (e.g., organismal properties determine properties of a monophyletic group by functional or epigenetic constraints).
3. Typology has had a strong influence on evolutionary thinking. The great advance of Darwinism and neo-Darwinism lies in the breakdown of typology. The move toward population thinking eliminated the static view of taxa as immutable entities. This was especially true of the species concept, which then acquired a biological and materialistic basis.

4. In the twentieth century, macroevolution as a paroxysmal process was championed by evolutionary biologist Goldschmidt and by paleontologist Schindewolf. Both believed in sudden evolutionary change, and Goldschmidt postulated a series of "systemic mutations" that produced hopeful monsters. Speciation was believed to result from such mutations, and, therefore, intraspecific variation was meaningless in evolution. Both theory and data were incompatible with this notion, and Goldschmidt's ideas fell rightfully into disrepute. He also, however, described how developmental (physiological) genetics could be used as a tool to study directions of evolution, and this field has been revived with considerable success in recent years (see chapter 4).
5. Twentieth-century evolutionary biology was marked by four important periods. The rediscovery of Mendelian genetic transmission provoked a debate between those who believed that mutations drove evolution and those who saw evolution as a process dominated by natural selection operating on small degrees of variation. It was later appreciated that mutations generated variation, whereas natural selection, migration, and drift determined the disposition of genes in population. The neo-Darwinian period, dominated by Wright, Fisher, and Haldane, gave us the theoretical underpinnings for understanding the fate of variation in natural populations. The Modern Synthesis accomplished the elimination of unlikely notions, such as orthogenesis, and spread the neo-Darwinian ideas to systematists and ecologists. In the period since the Modern Synthesis, it has been suggested that molecular variation in natural populations is neutral, objections have arisen to the primacy of natural selection, and the discovery and development of molecular genetics has enriched our understanding of the nature of organic variation.
6. George Gaylord Simpson brought paleontology out of an obsolete era, dominated by beliefs in orthogenesis. He melded population genetics with paleontological data and concluded that there were no incompatibilities. During this period, paleontologists became interested in correlating temporal changes in diversity with changes in earth history, and several found that massive radiations and extinctions were the rule. A variety of hypotheses were proposed to explain these major changes, some involving catastrophic events. More recently, it was suggested that paleontological data were incompatible with some supposed expectations of population genetics and neo-Darwinism. In particular, it was suggested that speciation was the motor behind evolutionary change and that most species were static throughout their history. This suggestion evinced a large-scale research program on evolutionary changes at smaller paleontological time scales. At present, many paleontologists still feel that the fossil record requires a major alteration of evolutionary theory, whereas others either see no conflict at all or feel that the challenge itself is weak and unsubstantiated.
7. Current macroevolutionary research has focused on the beginnings of animal evolution. The nature of Cambrian Explosion has been illuminated by new discoveries of animal fossils that have expanded our understanding of phylogenetic relationships, whereas clarifications of stratigraphy and geochronometry have made the case for an apparent appearance of animal life as a true evolutionary explosion.

CHAPTER 2

Genealogy, Systematics, and Macroevolution

> Our ancestors cut off the brightness on the land from above and created a world of shadows…
>
> – Tanizaki Junichiro

Systematics and Macroevolutionary Hypotheses

Why we need to connect the study of genealogy to systematics. A genealogy connects the members of a set of individuals or taxa by a criterion of relationship by descent. Owing to extinction and to lack of preserval of many fossil species, any hypothetical genealogy is likely to lack many taxa and all we can hope to do is draw the relationships among the remainder. The object of systematics is to produce a classification of taxa; genealogy may be one of several criteria used to construct the classification, but our real classifications of various taxonomic groups are based on a mixture of criteria, unified only by a hierarchical structure. I will argue forcefully that any systematic scheme should be congruent to the genealogical relationships we can establish. I have to admit, however, that the acquisition of molecular data in recent years has caused the reports of genealogies to outstrip our capacity, and perhaps even our will, to incorporate them into systematic schemes.

The need to unify systematics with genealogy is very clear upon reading articles on diversity change in the fossil record. Systematics creeps into macroevolution because of the *taxic approach* to analysis, in which the comings and goings of taxa at given levels (e.g., family) are recorded as extinctions and appearances, which are converted to rates (e.g., Newell 1952; Sepkoski 1993). It is impractical to identify or record the comings and goings at the species level, so some higher taxonomic level is necessary as a surrogate (Sepkoski 1978, 1979, 1993). As the taxonomic level decreases, taxon richness may more and more approximate species richness. But as taxonomic level rises, something else is most certainly being measured when we record origination and extinction rates (Valentine 1969). For example, Sepkoski's (1978) report on marine ordinal diversity demonstrates an apparent rise in richness through the mid-Paleozoic, followed by an approximate plateau to the present. This is clearly not the case for families or genera (Sepkoski 1984, 1993), which may slow down in their increase in the Paleozoic but increase steadily from the Mesozoic to the present. Perhaps ordinal level taxon richness represents adaptive zones (Van Valen 1984) whereas lower levels approximate species richness.

Although there have been some heartening changes since the first edition of this book, a few paleontologists have avoided the obvious need to define the meanings of taxonomic levels, genealogical reconstruction, and systematics (e.g., Gould 1989). Genealogical aspects of systematics have been largely ignored in studies of taxonomic longevity, diversity, and rates of taxon turnover (e.g., Sepkoski 1981; Van Valen 1973b; Valentine 1969). This omission weakens the clarity of macroevolutionary hypotheses, which often involve explanations of change between sets of character states in different taxa. A now celebrated example is the so-called extinction of the dinosaurs, whose characters did not become extinct if you accept the idea that birds descended from one dinosaur group. Genealogical considerations therefore muddy up the waters of what extinction really means.

A reliable pattern of genealogy must therefore be established before hypotheses of process and transition can be posed (Cracraft 1981; Eldredge and Cracraft 1980; Smith 1994). It may be preferable to keep genealogical reconstruction and classification as separate enterprises, but reality steps in. The language and thought processes of evolutionary biology are enmeshed in the language and practices of systematics.

The influence of systematic philosophy. The taxonomic hierarchy lends itself to a level-specific approach of hypothesis formation. This has been commonplace in macroevolutionary studies. Two well-accepted macroevolutionary hypotheses illustrate this well. First, it has been claimed that the phyla "appear" first in the fossil record, whereas lower taxonomic units follow. Second, different taxonomic levels have been said to have differing patterns of response to environmental change; the frequency of response decreases as the taxonomic level increases (e.g., Valentine 1968, 1969).

Remoteness in time could influence the assignment of two taxa to different taxonomic groups of equal rank. Raup (1983) found that the mean geologic age of first occurrences of the 27 readily preservable class-level taxa of marine invertebrates is 533 million years. Twenty of the 27 taxa first occur in the Cambrian at the time of this study. Because high taxonomic rank is based on genealogical relationship, overall similarity, and species richness, it is not clear whether this early origin is a function of true early morphological diversification or just an inherent property of higher taxa, whose early origins are bound to make them subtend many subordinate taxa that arise by branching of the stem taxon. But it is not unusual to draw an equivalence between high taxonomic rank and fundamental body plans or occupancy of major adaptive zones (Gould 1989; Simpson 1944, Valentine 1969, Van Valen 1984).

A strictly genealogical approach might trivialize the observation that "phyla appear first" into a tautological restatement of the systematic philosophy (Figure 2.1). Phyla might represent the first taxonomic split in the clade's history. If overall resemblance is used in delimiting phyla, then the hypothesis that "phyla appear first" would have a different significance. Here, we could say that major phenetic

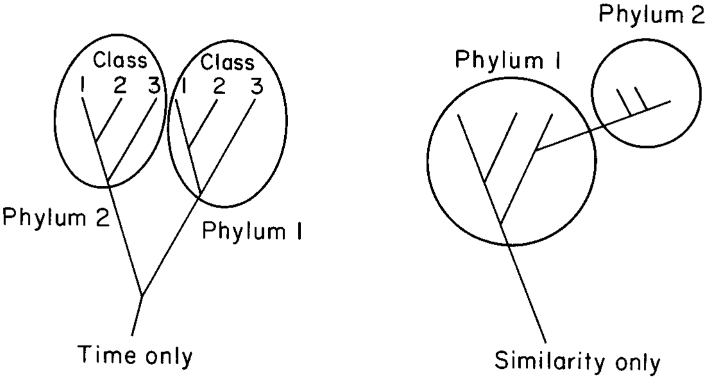


Figure 2.1. Two different classification schemes. On the left, phyla are delineated on the basis of time of branching. On the right, phyla are designated on the basis of dissimilarity, which increases on a horizontal scale.

differences materialized early in the history of life. Derived taxa might be limited in their potential to give rise to new taxa of phylum rank. Alternatively, special significance might be assigned to phylum-defining characters, which might be assigned more weight than others. Thus, some might assign more weight to the acquisition of *Hox* genes in the arthropods and allies than genes for specification of the number of bristles on the abdomen of a fly.

A similar argument can be made for the hypothesis that differing taxonomic levels each have their unique responses to changes in the earth's history. To the degree that morphological similarity defines the taxa, definitions of increasingly lower taxonomic levels would correspond to increasing homogeneity of ecological response to environmental change. As the taxonomic level increases, one tends to include more and more phenotypically different groups with differing ecological responses. If we group more and more phenetically different groups together into increasingly higher taxa, it stands to reason that this synthetic higher taxon will survive longer and taxa of this level will have a lower frequency of response to environmental change.

If genealogy is the only criterion used to establish classifications, then differential patterns of response by different taxonomic levels may have a different meaning. For example, more inclusive taxonomic levels may inevitably involve greater spans of geological time. The lower frequency of response of higher taxonomic levels may therefore represent a "buffering" response. Higher taxa are bound to have a lower extinction rate than lower taxa, but this may have nothing to do with morphological specialization (as in a phenetic classification); it may be only an inherent property of the taxonomic structure, where more inclusive and diverse taxa are bound to be more longevous (Flessa and Jablonski 1985). In the genealogical end member case, a mixed result is also possible. With time, a taxon may become morphologically diverse, ecologically diversified, and geographically widespread as cladogenesis proceeds. This would also confer on the inclusive taxon buffering against extinction. On the other hand, a strictly genealogical framework might also reveal that larger taxa in some cases have greater morphological diversity than others of comparable branching structure.

Advantages of the Genealogical Approach

Genealogies and character transitions. A framework established from a genealogical algorithm permits a useful analysis of character variation in the context of macroevolutionary hypotheses. Many macroevolutionary hypotheses attempt to provide mechanisms to explain differential taxon longevity. Claims that taxon longevity depends on biogeographic range (e.g., Boucot 1978; Jackson 1974; Levinton 1974) or that taxon longevity is the result of differential speciation rate or survival of species (e.g., Stanley 1975; Vrba 1983) may depend partially on the nature of character variation within the clades under consideration. In many cases, adaptations of individuals influence the susceptibility to extinction of species and larger taxa. Although speciation rate may ensure survival of a taxon, the possession of certain characters may permit an entire clade to outlast others or might permit descendants of a given clade to invade a new habitat. The testing of such ideas requires a mapping of character transformations on genealogies.

Consider the following hypothesis: Phenotypic evolution occurs because of species selection (Eldredge and Gould 1972; Stanley 1975). Levels below and above the species level are thus irrelevant to the evolutionary trend, which is a net change in character states over time. Take a hypothetical phylogeny of bivalve mollusks (Figure 2.2). A species bears character state *A1,* representing a compressed elongate shell, and character state *B1,* representing lack of ornamentation. The clam therefore has a morphology compatible with rapid burrowing in soft substrata (Stanley 1970). Let the ancestral species split into two daughter species. A split of each daughter species results in four taxa. Extant taxa T1 and T2 bear the ancestral character states *A1* and *B1.* Extant taxa T3 and T4 also bear state *A1*; they, however, have acquired character state *B2,* representing heavy ornamentation.

From a functional morphological point of view, the ancestral character state *A1* interacts with the state of character *B,* which determines the derived state defining the genealogical groups {T1,T2} and {T3,T4}. Let us call these two taxa "genera." In

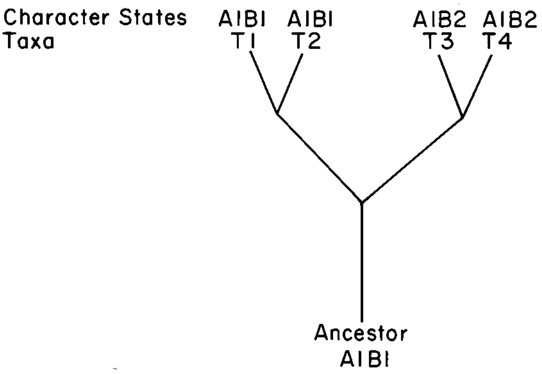


Figure 2.2. Hypothetical phylogeny of a lineage of bivalves. See text for explanation.

our specific example, *A1,B1* is a functionally compatible character set, whereas *A1,B2* joins two character states that would fail to be functionally harmonious under most circumstances. Squat shells with ornamentation would be preferable in stabilizing the shell on the bottom in swift currents, whereas elongate, compressed shells lacking ornament would be efficient in burrowing. The *A2,B1* state is a mixed case, not much good for either function. It would therefore surprise no one if the group {T3,T4} had a higher probability of extinction. Indeed, its evolution probably would have occurred under atypical environmental circumstances.

With this example, we can make several points about the role of functional morphology in predicting relative extinction rates and the basis of extinction. First, the character *A* defining the {T1,T2,T3,T4} group interacts with the state of the character defining the two included groups. The genus level of response to extinction may be defined by the special set of characters *A1,B2,* but character state *A1* will survive in either of the two taxa: {T1,T2}, {T3,T4}. Thus, taxon mortality at the genus level explains selective loss of the *A1,B2* character complex. But this surely is not an emergent phenomenon of the genus level, as we have defined it. The inevitable retention of the *A1* character state, moreover, is not readily identified with any taxonomic level. Indeed, it is only a matter of coincidence that selection among genera has occurred. Selective mortality can be reckoned from a simple summing of character states. Species become extinct *because of the character states they bear*; a conclusion that genus-level selection occurs is therefore ambiguous. We can at least, however, identify the taxonomic level at which the crucial combinations of character states result in differing probabilities of extinction.

An improved degree of focus thus emerges from a genealogical approach based on character analysis. At present, a disturbing vagueness plagues the literature. This has been reinforced by the use of taxonomic survivorship curves at many taxonomic levels, with a varied mixture of ecological and evolutionary intents. Levinton (1974), for example, employed the generic level to contrast paleoautecology with taxonomic survivorship among groups of bivalve mollusks. But the generic level was chosen as a matter of convenience, controlled by the available monographic accounts of the Bivalvia. This particular taxonomic level, which did reveal significant differences among bivalve groups, may be irrelevant for the purposes intended, simply because the character complexes involved in autecological aspects of taxon survival were concentrated at another level.

In a similar vein, variance in gastropod form has been found to decrease from the Paleozoic to the present (Cain 1977; Gilinsky 1981). This trend indicates that those taxa deviating from a modal form have tended to become extinct. Is this species selection, as claimed by Gilinsky? Of course species have become extinct. But the selection must be at the taxonomic level corresponding to the acquisition of the set of relatively poorly surviving character states. This may be at a much higher level than that of species and can be properly defined only once a character analysis is done, set against a genealogically based systematic framework.

Genealogical and systematic philosophies. Genealogical investigations may have at least four objectives, which are often intermixed. A *character analysis* is a study of features of individuals that may be used to construct a classification. The algorithm used to perform the character analysis may be qualitative or quantitative. A *genealogy* is a network of branchings whose topology reflects the relationships by descent of the taxa under consideration. A *classification* is an ordering of taxa based on various criteria but usually resulting in a hierarchy of successively inclusive sets (species grouped into genera, which are grouped into families, etc.). The classification may or may not be concordant with the genealogy. Finally, a *phylogeny* is an inferred genealogical history of a group, hypothesizing ancestor–descendant relationships, biogeography, and so on. The genealogy is only part of the process of producing a phylogeny. Genealogies and phylogenies are hypotheses of relationships and history. To the degree that a classification is meant to reflect a genealogy, it, too, must be regarded as a hypothesis.

Systematics has occupied a central place in the posing and testing of macroevolutionary hypotheses. Most of the classic works in the field (Mayr 1942; Mayr 1969; Mayr, Linsley, and Usinger 1953; Simpson 1961) stressed the inherent complexity behind the traditional objectives of systematics. They agreed, however, that a useful classification should account for genealogy and morphological similarity. These two components lay behind *evolutionary systematics,* an approach that assigns taxonomic rank by means of genealogical position in a phylogenetic network and the amount of morphological divergence of a taxon from its ancestral lineage. Phylogenetic reconstruction is mixed with, or follows, classification. The two other major competing systematic philosophies take this mixed strategy to be undesirable.

Phenetics seeks to produce classifications on the basis of overall similarity alone (Sokal and Camin 1965; Sokal and Sneath 1963). Genealogy is not a necessary objective of phenetic classifications, although overall similarity must have some mapping to relationship by descent (Sokal and Sneath 1963). *Phylogenetic systematics* seeks to establish a network of genealogically based relationships with no overall similarity criterion employed for classification (e.g., Camin and Sokal 1965; Hennig 1966; Kluge and Farris 1969). Phylogenetic systematists seek to cluster *monophyletic groups,* or the entire descendant subset of taxa derived from a given ancestor.

Arguments over the preference for any of the three systems usually revolve around several desirable criteria of classifications used by evolutionary biologists:

1. *Convenience:* The system should yield a classificatory system that is not cumbersome and should be intuitive enough for all to grasp.
2. *Congruence:* Classifications based on different characters should yield similar results.
3. *Genealogy:* Most evolutionary biologists desire a classification that reflects evolutionary relationships.
4. *Naturalness:* Groupings should, in some readily understood sense, reflect directly the character states used to determine the classification (Gilmour 1961).

Constructing an Evolutionary Tree: A Cladistic Approach

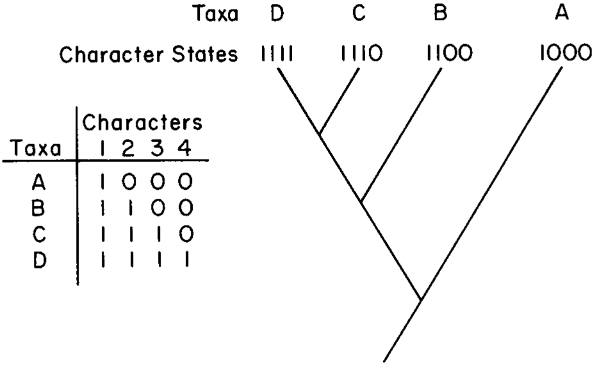
Phylogenetic systematics. The cladistic approach establishes networks of genealogical connections based on uniquely shared, and evolutionarily derived, similarities –

or *synapomorphies*. Any derived state is said to be *apomorphous*. Any ancestral state is said to be *plesiomorphous*. Overall similarity is thought to be misleading as a grouping criterion, as it often entails groupings by shared ancestral features that may define genealogically more inclusive groups, rather than specific and closely related derived groups.

The primary objective of cladistics is to map taxa onto a *cladogram* whose branchings signify genealogy and whose topology reflects solely the evolutionary changes in characters. Algorithms include hand-calculated groupings by use of synapomorphies (e.g., Hennig 1966), computer-based algorithms that attempt to find the tree with the smallest number of evolutionary steps (the method of *parsimony*) using various assumptions that make tree calculation somewhat more tractable (e.g., Camin and Sokal 1965; Farris 1970; Goodman et al. 1982), and character-compatibility algorithms that search for sets of characters whose states define the same genealogical relationships (e.g., Estabrook 1972, 1980; LeQuesne 1969). In some cases, phenetic distances have been modified to construct genealogical relationships (e.g., Farris 1972; Felsenstein 1982; Fitch and Margoliash 1967). A second objective of cladistics is to use the genealogy to produce a classification that best represents the branching pattern.

Hennig crystallizes the problem. Hennig's *Phylogenetic Systematics* (1966) helped to focus most current attempts to understand genealogical relationships among taxa and to derive classifications that map logically to genealogical trees. Speciation, the splitting up of one species into two or more daughter species, is the basis for the whole system. After a number of splits, groups can be defined as a series of increasingly more inclusive nested sets (Figure 2.3). Species are related by the branching network created by the cladogenetic process. A *monophyletic group* is thus "a group of species descended from a single (stem) species, and which includes all species descended from this stem species" (Hennig 1966, p. 73).

As cladogenesis occurs, *characters,* attributes of the organisms, change in their respective *states*. The problem is how to use character data to reckon genealogy.



Taxa	Characters 1 2 3 4
A	1 0 0 0
B	1 1 0 0
C	1 1 1 0
D	1 1 1 1

Figure 2.3. A matrix of character states by taxa, with a cladogram, established by Hennigian principles.

Many of the taxa produced have become extinct, so that we can never establish the complete network of ancestors, nor do we have an extant record of the magnitude of character transitions throughout the cladogenetic history of the group under consideration. All we have are the extant and fossil taxa, and their character states.

Groups with uniquely derived character states, *autapomorphies,* are the most closely related. Successively more distantly related groups are connected by their shared derived character states. An increasing number of synapomorphies increases the likelihood that a grouping is genealogically circumscribed. Grouping by shared ancestral characters invites the danger of producing groups that are genealogically incomplete. Figure 2.3 shows that the synapomorphies identify monophyly. Nested sets of synapomorphies define the total tree of relationships of monophyletic groups, such that some monophyletic groups are nested within other more inclusive monophyletic groups. The ability to group taxa into nested sets, on the basis of synapomorphies, would be easy if all characters mapped compatibly on a tree. As we shall see, incompatibility of character states is the fundamental problem in genealogical reconstruction.

Character correspondence between taxa and homology. If we state that two taxa have the same character, we imply that we have a criterion for mapping correspondence of the character in the two taxa. This correspondence is known as *homology,* and it implies a common evolutionary history for the characters in the two taxa, respectively. Criteria for homology must be established, so that features of related taxa can be identified as states of the same homologous character.

The biological explanation of homology must be sought at four levels of types of characters (Abouheif 1997):

1. Gene
2. Gene expression
3. Embryonic origins
4. Morphological structures

If there was a simple mapping between these four elements, then perhaps all character types could be mapped simply and congruously onto a cladogram. But there is ample evidence that these four levels may have complex interrelationships. Genes, for example, may have pleiotropic effects. Thus, several morphological structures may be affected partially by many genes, and one gene may affect many morphological structures. Over evolutionary time, a morphological structure located in a readily identifiable position might be affected by a different suite of genes. A similar argument can be made for patterns of gene expression. Many of the genes that are involved in fundamental determinations of early anteroposterior and dorsoventral orientation also are expressed and presumably are active in many other developmental events (see chapter 4).

This degree of variation argues for a tree-based definition of homology, favored by cladists. Homologous characters are those that are consistent in determining evolutionary relationships. Mechanisms behind homology, however, involve the four levels mentioned above, and we can imagine a variety of hypotheses that might lead to congruence among characters or others that might lead to homoplasy. A gene's function in a developmental pathway might be co-opted to effect a new morphological feature. The gene's expression patterns may now be more complex and a tree might have to now require an additional step to explain the pattern of character evolution. From the perspective of the tree, this character would no longer be homologous, but obviously *mechanisms* behind homology could be invoked to explain the new tree.

To understand the interrelationships between the four levels, it is very helpful to map the history of effects at these four levels onto a tree (Figure 2.4). Thus, for

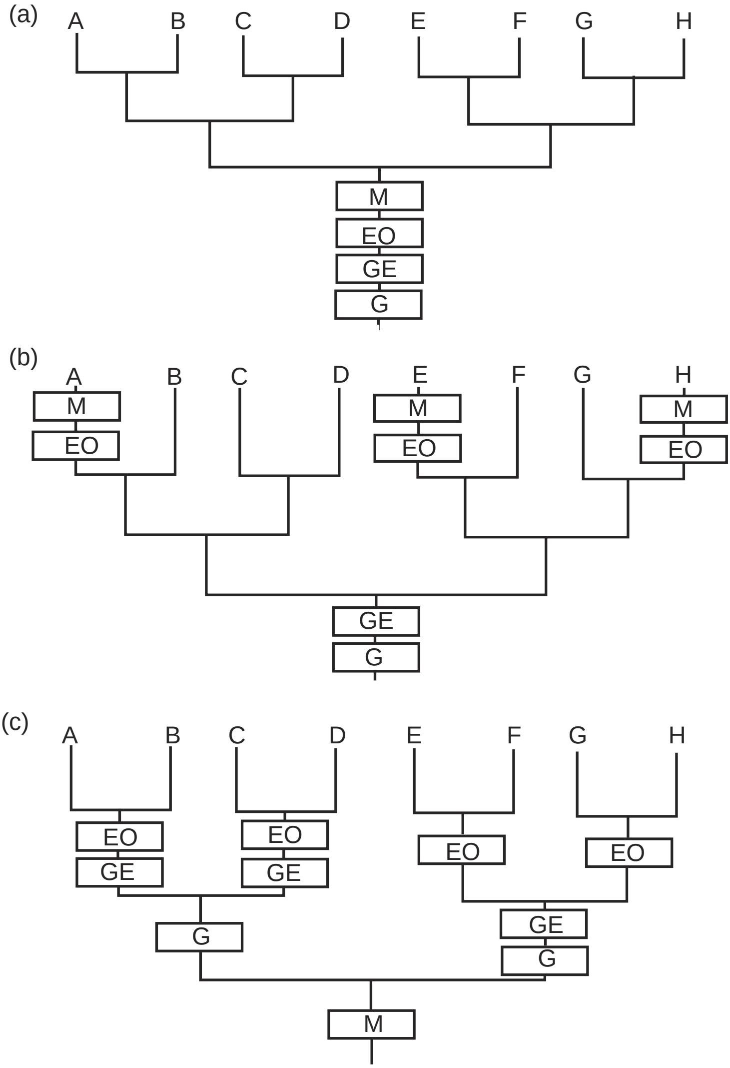


Figure 2.4. Three evolutionary scenarios associating gene structures (G), gene expression patterns (GE), embryonic origins (EO), and morphology (M): (**a**) the developmental integration of characters; (**b**) a scenario of developmental opportunity; (**c**) the fixation of a morphological trait, despite variation in fixation of other genic and developmental traits. (From Abouheif 1997, with permission from Elsevier Science.)

example, we can show that a gene such as the homeobox gene *Distal-less* is a do-all functional gene, expressed along the proximal–distal axes of a wide variety of developmental systems, including vertebrates and arthropod limbs, polychaete parapodia, and echinoderm tube feet (Lowe and Wray 1997; Panganiban et al. 1995, 1997).

In practice, the homology of phenotypic characters is rarely traced by systematists to the underlying genome (except in studies of molecular evolution). Tests for homology should involve the following criteria (Patterson 1982):

1. Two homologous character states may not exist within one organism. Different character states might exist among organisms of a single taxon or species.
2. Two character states in two organisms are of the same homologous character if they occupy the same topographic or ontogenetic position in the organism.
3. A series of character states in a series of corresponding taxa belong to one homologous character if the cladistic relationship among the taxa, defined by the character, does not contradict any genealogy defined by "truly homologous" characters.

The last two criteria require qualification and suggest other criteria. Criterion two implies that homologous characters can be "located" in different taxa. This ability is strengthened to the degree that (1) evolution produces unique phenotypic sites and (2) evolution is slow. If evolution is very rapid and not unique (i.e., convergence is common), then the ability to identify the phenotypic expression of corresponding parts of the genome is erased. Location can also involve a temporal aspect, especially because ontogenetic data can be applied to systematic problems (e.g., Alberch 1985; de Beer 1958; Nelson 1978).

A special set of instances may directly link homology and polarity. Developmental anomalies often reveal seemingly ancestral states. In rare instances, whales have complete limbs similar to those used in walking ancestors, despite the fact that millions of years have elapsed since the structures related to walking were presumably lost (Andrews 1921; Lande 1978). The atavistic appearance of long-lost structures in amazing detail (e.g., Andrews 1921; Kurtén 1963; Marsh 1892) seems to discredit the belief that the loss of a structure implies the loss of the genes, as a naive version of an adaptive theory of evolutionary genetics would predict (Kollar and Fisher 1980). This suggests that for whatever reason, the genome is to a degree stable and a genetic basis for homology is possible. It also suggests another criterion for homology:

4. Two states in two organisms can represent states of a homologous character if a developmental anomaly in one taxon produces an individual with a state largely similar to the other taxon, in the same topographic position.

This criterion must be used judiciously, because the simplicity of a character state might result in the evolutionary convergence of states of a nonhomologous character. For example, if two states represented different colors of a butterfly wing of two respective species, the appearance of taxon *B*'s color, as a variant of taxon *A*, cannot guarantee homology. Complexity of similarity is therefore an essential element of this criterion. Unfortunately, it is difficult to define a mathematical function that relates the probability of homology to increase of similarity. One of the *bithorax* complex phenotypes (see Ouweneel 1976) in *Drosophila melanogaster* mimics the presumed ancestral state of the Diptera (i.e., two pairs of wings). There is no reason to believe, however, that this is the particular genetic route backward to the ancestral state. Appeals to strong similarity of detail, therefore, are intuitively attractive but no more than that.

Patterson's (1982) third test of homology, compatibility with other homologous characters, raises both the fundamental strength and an important weakness of the Hennigian cladistic method. This criterion implies that homology is a hypothesis, rather than a proven statement of genealogical connection among character states. The hypothesis of homology for a given set of character states is therefore corroborated if the genealogical relationships defined by synapomorphies does not contradict others defined by other characters. Homologies of several discrete sets of character states are thus reinforced to the degree that the corresponding genealogical relationships defined by the discrete sets are compatible. But what if sets of states produce incongruent inferred genealogies? How do we decide among different trees defined by different characters, and how do incongruities affect our hypotheses of homology?

The first criterion of homology, that a character not be found in two different locations on the same creature, implies that we are excluding serial homology from our discussions. Many structures – genes for example – arose in evolution by duplication. In the first descendant taxon with a duplication, there is an ambiguity in that two structures are homologous with one belonging to the ancestor. Subsequently, the ontological ambiguity of homology disappears, but there is still an epistemological confusion in the status of the relationships between the repeated structures within the same individual (e.g., two tandem genes that arose by duplication that now serve different functions). This confusion is heightened when the duplications affect the same phenotype in different ontological stages. Thus, *Drosophila melanogaster* has larval and adult alcohol dehydrogenases that presumably serve the same function but the same structural gene codes for both enzymes; the difference is an upstream sequence. In this case, the distinction between serial homology and evolutionary homology breaks down, without an ontogenetic criterion.

If our objective is genealogical reconstruction alone, then it is not clear whether the genotype–phenotype distinction is all that important. Characters are characters, and homologies can be established – indeed they have been established for hundreds of years – without the benefit of knowing the genetic underpinnings. Genetic data, such as nucleotide sequences, are also sources of homology, as long as some sort of criterion of location can be employed. One must be sure, for example, that one is following the same gene through a genealogy if the sequence is to mean anything. The connection between genes and phenotype becomes important when one is interested in tracing given characters in clades, particularly with regard to evolutionary mechanism. If one believes in genetic constraints, then the DNA history is as important as a phenotypic history. This connection is most crucial if we are ever to understand the relative contributions of developmental, genetic, and functional constraints to phenotypic evolution.

Cladograms and phylogenies

Definition of cladogram. A *cladogram* is a diagram posed as a hypothesis of the genealogical relationships among a series of taxa, grouped by their synapomorphies. A *phylogeny,* by contrast, is a hypothesis depicting the exact history of the evolutionary connections among the taxa. It may invoke a specific extinct ancestor that is not preserved as a fossil. I illustrate the distinction between a cladogram and a phylogeny in Figure 2.5. For the two-taxon case, we assume that one or the other might be an extinct species. Note that five possible phylogenetic histories can be derived from the simple cladogram connecting taxa *x* and *y* (see also Eldredge and Cracraft 1980; Platnick 1977).

With some information on polarity of character states, we can restrict the phylogenetic hypotheses somewhat. Consider three characters whose states are 0 (ancestral) or 1 (derived). Then imagine a root to the cladogram, defined by the most ancestral character states {0,0,0}. If we refer to the cladogram in Figure 2.5, with the additional information on polarity, then the possible phylogenies are restricted to types *a, c,* and *d.* In case *c,* an ancestor is invoked who bears the character states {0,0,0}.

When we consider three taxa, the notion of ancestral and derived character states is better defined (see Nelson and Platnick 1981 for extended discussion). Three-taxon statements devolve to the problem: Are two of the taxa, *A* and *B,* more closely related to each other than to another taxon, *C* (Figure 2.6)? The most distantly related taxon is defined as that one which joins in the cladogram, after uniting the first two, which share the most derived states over all characters.

A cladogram is constructed from a matrix of taxa by characters such as the one in Figure 2.7. For this matrix we assume that 0 is the ancestral (plesiomorphic) state and that 1 is the derived (apomorphic) state. Figure 2.7 shows the cladogram based only on characters 1 through 4. The cladogram has a *root,* which is defined by the most plesiomorphic states for all characters.

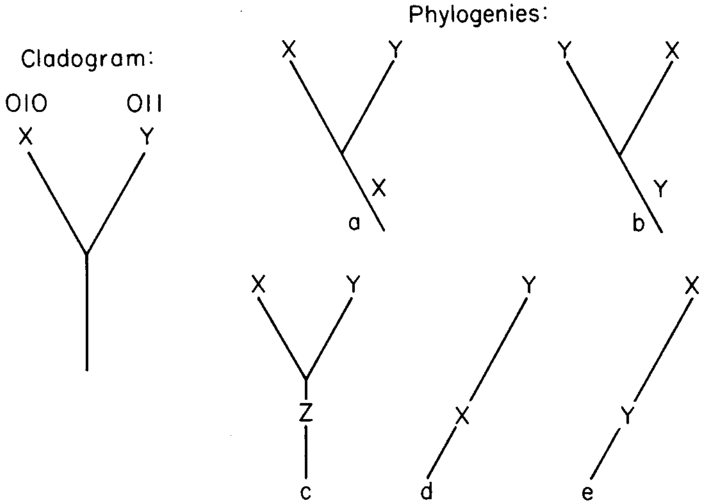


Figure 2.5. Cladograms and phylogenies: a cladogram for two taxa, with the possible phylogenies that might be implied.

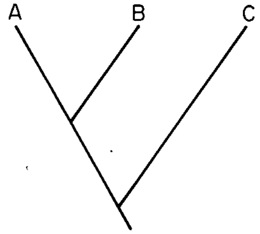


Figure 2.6. A three-taxon cladogram.

Note that characters 5 and 6 define a group that is inconsistent with the rooted cladogram. One might conclude that the inconsistency falsifies the hypothesis of relationship derived from the majority of the characters. We might favor the cladogram as illustrated in Figure 2.7, as the information from four characters defines the cladogram, whereas the inconsistent hypothesis is defined by only two characters. This is often characterized as the adoption of the *least refuted hypothesis* (e.g., Lynch 1982). It is used typically by those who employ nonnumerical algorithms to generate rooted cladograms. These inconsistencies are the crucial problem in the resolution of evolutionary relationships and are discussed further below (see Homoplasy: The Fundamental Problem)

Rooting the cladogram. The construction of a root for a cladogram is one of the most difficult problems of phylogenetic systematics. One needs a criterion to locate the part of the cladogram that bears the most ancestral states. This requires a criterion for identifying ancestral character states. Two main ones have been employed: *outgroups* and *ontogeny.* In a three-taxon case, one taxon is more distantly related than two others that are more closely united by synapomorphies. Cladograms can be constructed by successive additions based on three-taxon statements (see Nelson and Platnick 1981; Wiley 1981, but also see Nelson and Platnick 1991; Platnick, Humphries, Nelson and Williams 1996). The choice of an outgroup involves picking a character or set of characters that is widely agreed to have more ancestral states than is present in the first three taxa. Thus, an outgroup for the bivalves might lack a shell but have spiral cleavage and a mantle. Its attachment to the cladogram defines polarity.

	Characters					
	1	2	3	4	5	6
Taxa						
A	1	1	0	0	0	0
B	0	0	1	0	1	1
C	1	1	0	0	1	1
D	0	0	1	1	0	0
E	0	1	0	0	1	1

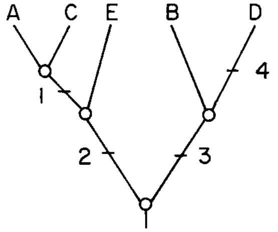


Figure 2.7. A matrix of character states by taxa for a hypothetical group. For each character, 0 is taken to be ancestral and 1 is derived. At right is a Hennigian analysis for characters 1 through 4, which are compatible. Character numbers on tree define groupings delineated by the next highest node (e.g., group [A,C] is defined by character 1; [A,C,E] is defined by character 2).

The use of *ontogeny* derives from Haeckel's biogenetic law that ontogeny recapitulates phylogeny (Nelson 1978). The reality of the biogenetic law has long been in hot dispute (see discussion in Gould 1977). This criterion could only have utility if evolution by terminal addition occurs and either descendants comprise a simple addition of the stages or a form of acceleration compresses the stages into the same developmental period. Alternatively, an extension of Karl von Baer's laws of development into evolution (von Baer didn't believe in evolution) pose hypotheses of polarity (Nelson 1978; Patterson 1982). General (ancestral) features are believed to occur early in the ontogeny of related taxa. Later ontogenetic stages represent specializations (derived states). This hypothesis supposes implicitly that early stages of ontogeny are less subject to evolutionary alteration than later stages. See chapter 4 for further discussion of this issue.

Ontogenetic considerations show that apparent ancestry cannot be identified under certain conditions (Fink 1982):

1. When the common ancestor of two taxa evolved state *b* by adding a stage to the ontogenetic trajectory, but one of the two descendants went to state *a* by loss of the terminal state *b*
2. Same as condition 1, only ancestor exhibits acceleration and one descendant shows slowing of development
3. Same as condition 1, only contrasting a movement up in onset of development in an ancestor, followed by relative delay of onset in development of the descendant

These three conditions will erase the record of character polarity. Any shuffling of stages within a sequence would destroy the directional utility of the ontogenetic order of the character states in descendants.

Alberch and Gale (1983) have investigated ontogeny in frogs and salamanders and demonstrated that developmental regularities might be a valid key to character state sequence. During development, digit number one is the last to appear in the frogs *Xenopus laevis,* whereas digit number five is the last to appear in the axolotl, *Ambystoma mexicanum.* This seems to correspond to evidence for evolutionarily derived digit loss. The last digit produced during ontogeny is that one which is lost first. This cannot be used to determine polarity, but at least a predicted sequence defining a linear order of character states in evolution might be established from such data. Evolution could go in either direction along the sequence. Another encouraging example is McGowan's (1984) study of the development of the avian tarsus. It had been previously suggested that ratites were derived from carinates (flying birds) by an arrest of development. Carinates, however, can be shown to have an ontogenetically unique pretibial bone, whereas the ratites share the ascending process of the astralegus with the theropod dinosaurs. Ratites therefore are in a relatively ancestral state and their ancestral stock is thus more ancestral than that which defines the flying birds.

It is likely that many evolutionary sequences involve terminal addition – or at least resolvable alterations of developmental sequences. Alterations of ontogenetic sequences, particularly terminal addition, have been suggested in several studies of fossil mollusks (Fisher, Rodda, and Dietrich 1964; Miyazaki and Mickevich 1982;

Newell 1937). The evolutionary adjustment of ontogenetic patterns in the tropical American salamander genus *Bolitoglossa* is another example. Hand and foot morphology of the species represents all stages of intermediacy between the slightly webbed, large-digited structures of the upland species and the diminutive fully webbed small-digited ones of the lowlands (Wake and Brame 1969). Diminutive lowland species are paedomorphic and seem to result from the retention of juvenile characters of the larger ancestors in the adults of the smaller descendants. The webbing and small size seems adaptive for the relatively more arboreal habit of the lowland forms (Alberch 1981; Wake and Brame 1969).

In his functional study, Alberch (1981) identifies the plesiomorphic state for the genus *Bolitoglossa* by an outgroup comparison. The outgroup is intermediate along the ontogenetic track, relative to the two derived species he considers carefully. Thus, the root of the network (not done by Alberch in quite this manner or with this terminology) is near a point where species bear intermediate character states of the ontogenetic track. We must assume, therefore, that reversals are possible; one can move backward or forward along an evolutionary–ontogenetic trajectory. But suppose that we had no good outgroup for comparison. It is likely that the network might be rooted (if only ontogenetic characters were employed) near the taxon with the greatest representation of early ontogenetic character states. Given our information, this could lead to incorrect judgments about the history of the group. We can imagine two closely related sister taxa whose difference rests on one synapomorphy. If most of the useful characters are associated only with ontogeny, and one cannot be sure as to the ancestral state of any character, only the sequence, then it may be difficult to root one group with respect to another. In other words, a conflict in rooting cladograms might arise between the use of outgroup comparisons and ontogenetic character sequences.

If there is a correlation between the order of ontogenetic stages and the stratigraphic sequence, then we would be justified in invoking fossil sequence as corroborative evidence favoring rooting of the network near the species that is both stratigraphically oldest and ontogenetically "earliest" (Miyazaki and Mickevich 1982). This conclusion is based on the sensible argument that it is more likely that evolution has proceeded forward in time, rather than backward.

The Problem of Ancestors. The root of cladograms provides information on the nature of ancestry but does not define ancestors. Consider the cladograms and possible phylogenies in Figure 2.5. In many cases, the ancestor will never be identified, simply because no independent criteria would delimit a choice among the possible phylogenetic hypotheses. In these cases, the study of macroevolution is restricted to the study of the possible mode of transition from a taxon to its closest relative. We can only speculate about what combination of character states ancestral transitional taxa might have borne.

Homoplasy: the fundamental problem

Definition of homoplasy. The resolution of incongruencies of certain characters, or *homoplasy,* requires us to discard certain characters as bearing false witness to the evolutionary relationships of the group. Homoplasy can be defined as any resemblance between two (or among more) taxa that is not due to inheritance from a common ancestor (Simpson 1961, p. 78). Parallel evolution, convergent evolution, evolutionary reversals, mimicry, and chance evolution of similarity can all produce homoplasies. Parallel evolution could imply some common evolutionary constraint (see chapter 4) due to common ancestry of two now-distant taxa, which causes separated lineages to develop along similar phyletic paths. Convergence can cause us to mistake homologous for *analogous* structures, or features of two taxa that are similar, but not because of a common evolutionary connection.

As the degree of homoplasy increases in the evolutionary history of a group, the degree of inconsistency with the same tree among different characters must also increase. No one would doubt that homoplasy occurs; indeed, character inconsistency is the rule rather than the exception (see Felsenstein 1982). As mentioned above, the concept of minimum refutation, or maximum corroboration, arose from this problem.

Some approaches to the homoplasy problem. We can attempt to minimize the blurring effects of homoplasy by at least two approaches: *character compatibility* and *parsimony.* Character compatibility involves choosing a majority set of internally consistent characters to construct the genealogy and the classification. Parsimony acknowledges conflicts but chooses the cladistic network requiring the fewest character changes. With six characters or fewer, compatibility and parsimony give the same solution. Nonnumerical approaches usually attempt to establish synapomorphies and then drop characters that imply groupings inconsistent with the majority of consistent characters (e.g., Eldredge and Cracraft 1980). This is, with six characters or fewer, a compatibility analysis. Character sets may be excluded by appealing to various functional morphological considerations that might suggest convergence. Thus, J. D. Smith (1976) argued that wing characters in the bats are homoplasic for functional reasons and suggested that bats may be polyphyletic. Other nonquantitative studies compromise compatibility by sometimes accepting inconsistencies among characters (that require reversals in character state) to minimize the number of steps to make the tree.

The compatibility approach was formalized by LeQuesne (1969), who recommended that monophyletic groups be defined by *cliques* of consistent character states. Figure 2.8 shows a simple case, in which classification by use of secondary compounds is employed to produce a genealogical classification. We assume that evolutionary acquisition of the compound occurs only once and that absence is the ancestral state. As can be seen, two chemicals can be inconsistent with the same hypothesis of genealogical relationship. Numerical approaches have been developed, especially by Estabrook and colleagues (Estabrook 1972; Estabrook and Anderson 1978), to identify cliques of compatible characters to construct a rooted cladogram.

Parsimony presumes that the cladogram with the shortest number of steps will most likely approximate evolutionary relationships. Intuitively, this is an attractive idea that fits one's sense that Occam's razor resolves complex problems the best. Of course, it is completely possible that evolution could have occurred with more steps and that seemingly homoplasic characters are actually reflective of evolutionary his-

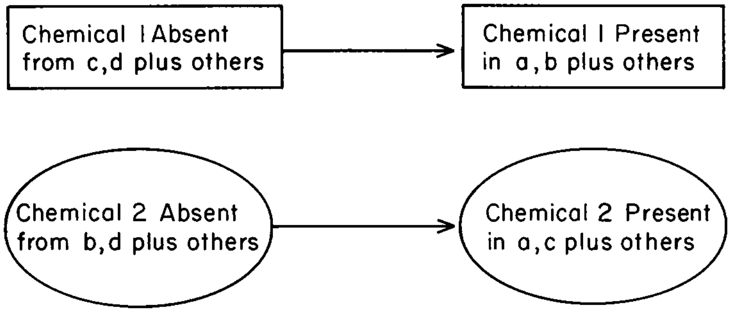


Figure 2.8. A hypothetical character compatibility analysis for secondary compounds in a set of plant taxa. The hypothesis that the occurrence pattern of chemical 1 is ideally related to the evolution of the group is incompatible with the hypothesis that chemical 2 is ideally related to the group's evolution. (After Estabrook 1980.)

tory. But without independent information, it seems more likely that minimizing the number of changes is the most likely explanation of evolutionary change. One must remember, however, that this is only a supposition, which is necessary if we are going to seek an algorithm that can optimize a solution.

Who invented parsimony? That is a fun question that is perhaps best left to historians and devotees. Hennig (1966) confined his computational examples to those where parsimony is not needed; all of his monophyletic groups were defined by character sets that were congruent. Followers of Hennig, who often call themselves cladists, have sought to find textual evidence that Hennig believed in parsimony (Farris 1983), but others also came to the commonsense conclusion that parsimony is the appropriate criterion to optimize, albeit with very different techniques (Camin and Sokal 1965; Eck and Dayhoff 1966; Fitch and Margoliash 1967). Farris pointed out that Hennig stated that homology should be first assumed for characters when inferring a monophyletic group, which amounts to the statement that homoplasy should not be presumed except where required. This, in effect, might be a statement of parsimony, but it might just as well be a statement of how to best define a single monophyletic group. Whether Hennig first thought of parsimony or not, it is fair to say that his followers developed and championed the concept (Farris et al. 1976; Farris 1979, 1983; Kluge and Farris 1969).

Parsimony is employed in both nonquantitative and numerical approaches (Camin and Sokal 1965; Farris 1970; Kluge and Farris 1969). We presume that the hypothesis of genealogy most likely to be correct is the one that requires the minimum number of evolutionary steps to explain the tree. Of course, nature doesn't have to be parsimonious; we simply claim that we will be correct most often by assuming the minimum number of steps. If the rate of evolution is very rapid and filled with reversals of character state, then the shortest number of steps may very well not be the correct phylogenetic solution. Should we then drop noisy characters and adopt a compatibility approach? Compatibility analysis can be criticized on the ground that it omits possibly informative data by dropping characters from the analysis. Although some characters have conflicts with the overall set, their use might contribute to some resolution, assuming that homoplasy is homogeneously scattered throughout the incompatible set. If homoplasy is known to be present in a few specific characters, it might be best to drop these from the analysis.

Camin and Sokal (1965) proposed a simple algorithm that depends on the knowledge of polarity of evolution among the states of any character. They assume that (1) characters can be expressed in discrete states, (2) states can be ordered, (3) the ancestral state arose once, and (4) evolution is irreversible. Several algorithms have been proposed to find the tree with the smallest number of evolutionary steps (Camin and Sokal 1965; Estabrook 1968; Sneath and Sokal 1973).

Another algorithm employing parsimony was suggested by Kluge and Farris (1969) and further developed by Farris (1970). The method, like that of Camin and Sokal, depends on the ability to code a series of states in some order, but reversals are permitted. Polarity needs to be known to root the cladogram. Alternatively, the characters can be coded as a series of states with no polarity. To root the tree, one then needs an outgroup to establish polarity of characters within the tree.

The data recorded in the form discussed above are in Figure 2.7. The distance between any two taxa is then computed as a city block, or Manhattan metric, which computes the degree of differentiation, the *advancement index,* of taxon *A* from *B,* as

$$d(A,B) = \Sigma_i \left| x(i,A) - x(i,B) \right|$$

where $d(A,B)$ is the degree of differentiation and $x(i,A)$ is the value of character state i, for taxon *A*.

Although taxa can be grouped in any order (see Farris 1972), the following algorithm (based on Kluge and Farris 1969; Wiley 1981, p. 182) starts either with the most "ancestral" taxon or with characters of a hypothetical ancestor or outgroup.

1. Specify an ancestor or sister group.
2. Compute D to ancestor for each taxon; find the taxon with minimum D. Connect taxon to ancestor, creating an *interval* for that taxon.
3. Find the next taxon with smallest D from ancestor/sister group.
4. Find the interval that shows least difference from this selected taxon. To find this, compute the difference between the selected taxon and the interval of each taxon that is already connected to the tree. If we have a taxon, *A,* for example, connected to an ancestor and our next taxon is *B,* then we compute:

$$D[B,INT(A)] = [D(B,A) + D(B,ANC(A))]/2$$

5. Attach the taxon to the interval with which it differs least. To do this, we construct a hypothetical common ancestor for the two taxa, such that the ancestor's character states are the median of the character states of the first taxon, its original ancestor, and the new taxon. Using the median allows the tree to satisfy the *triangle inequality* (the distance between any two taxa is less than, or equal to, the distance between the two and the sum of distances between each of the two, and a third taxon).

This algorithm leads to the cladogram depicted in Figure 2.7. In effect, it works by dropping the two incompatible characters. In complex data sets, the cladogram with the smallest number of changes must be found by calculating many trees and choosing the one with the fewest steps. In these cases, parsimony does not necessarily drop out incompatible characters, which may give some additional information that can minimize the length of the tree. Another algorithm is required for searching among many trees (e.g., Farris 1970). Various mainframe and microcomputer packages have become available in recent years to find the correct tree (e.g., the Phylip package of Joseph Felsenstein, the PAUP* package of David Swofford, and the Hennig86 package of J. Steven Farris). The notion of a correct tree, of course, is more than slightly loaded with controversy.

This algorithm has been found to be a usually most parsimonious method for establishing cladograms. It was the best method for approximating the phylogeny of the caminalcules when all characters were considered (Sokal 1983b). It performed more poorly than some phenetic approaches when smaller partitions of the characters were employed (Sokal 1983c).

The difficulty in parsimony lies with analyses of many taxa. Two problems crop up: computational time and a multiplicity of trees of similar numbers of steps. Tree-searching algorithms become exponentially more difficult as the number of taxa increases, and an analysis using a standard computer package may take days to find the shortest tree. Algorithms developed for this purpose are usually incapable of finding the shortest tree with large numbers of taxa and characters but instead use a reasonable search routine to find what is almost certainly close to the shortest tree. What is often vexing is the large number of trees that differ by just a few steps. Given that parsimony may not explain evolutionary transitions, one has a right to conclude that the absolute shortest tree may not be the best reflection of evolutionary relationships. Nevertheless, it is possible to get surprisingly good results, even with large data sets (Hillis, Huelsenbeck, and Swofford 1994).

Of greatest recent interest are the techniques that estimate cladograms by means of parsimony from molecular data (e.g., Eck and Dayhoff 1966; Fitch 1971; Fitch and Farris 1974; Moore, Barnabas, and Goodman 1976). In some cases, overall distance (e.g., number of amino acid differences) has been used to construct cladograms, as in the classic work of Fitch and Margoliash (1967). A fitting method is employed that minimizes the number of evolutionary steps on the constructed tree, relative to the total number of steps required to explain the original matrix of amino acid differences. Later approaches have employed parsimony to infer trees for both amino acid differences and nucleotide differences (e.g., Goodman et al. 1979, 1982). Gene duplications have been invoked to increase the consistency of characters on the tree (Goodman et al. 1982). We will further discuss molecular trees below (see Molecular Approaches to Genealogy Construction).

Efficacy of the cladistic methods. Felsenstein (1978, 1982, 1983) has discussed the conditions under which parsimony and character compatibility are likely to fail in producing an accurate genealogy. As might be expected, as the rate of evolution increases, the probability of reversals, convergence, and so on, may increase as well. This will tend to blur the tree and diminish the ability of uniquely derived states to identify monophyletic groups. As the degree of homoplasy increases, it becomes increasingly unjustifiable to have great confidence in the best solution (i.e., the shortest cladogram), although we would accept it as the best available hypothesis for the data at hand (see Sober 1983). If two adjacent branches of a tree are very long, then accumulated differentiation between the two taxa might be erased over time by character reversals (e.g., multiple hits at the same site positions in a nucleotide sequence). This process would spuriously reduce the degree of evolutionary distance between the branches, which might in turn result in their being wrongly grouped by a phylogeny algorithm. This phenomenon is known as *long branch attraction*.

The worst case is that of parallel evolution. Felsenstein (1978) showed that if parallel evolution is pronounced (due to either elapsed time or increased rate of evolution), over all characters, along two isolated branches of a phylogenetic tree, relative to another intermediate branch where the evolutionary change is less, the inferred tree will be incorrect. This can be visualized as an isolated and coordinated extensive change in unrelated lineages.

Coordinated and independent parallel evolution can be imagined when a series of characters are correlated, as in a set of characters that respond to one change as an integrated developmental unit (e.g., Gould 1982a). In this case, parallel evolution might cause the construction of the wrong tree. This may be common in studies in which several characters are used, and all are essentially a single response to the same primary change. Such a case seems to apply to the neotenous evolution of salamanders. Changes in one hormone may have induced the coordinated responses of blocks of characters, with some lack of harmony among the blocks (heterochronic evolution [Etkin 1970]).

The efficacy of various methods can be tested by two techniques:

1. Assessing how well the trees explain the character data. For example the retention index (RI) evaluates the efficacy of a tree in explaining character data by estimating the degree of homoplasy (Farris 1989). The proportion of taxa in a putative monophyletic group that retain a character designated as a synapomorphy declines as more and more members of the group lack the character, owing to later transformations or reversals. Thus, if the retention index is 1.0, all members of the group share the synapomorphy. This index is summed over all characters and varies from 0 to unity. It is important to remember that the RI tends to decline with increasing numbers of taxa, so one must contrast a measured RI with that which is typical of taxonomic groups of that size.
2. Simulating trees and assessing how well different algorithms use character data to deduce the correct tree, which is known by definition. Alternatively, one can take trees whose evolutionary relationships are known with some degree of certainty by one means (e.g., morphological) and compare them with trees deduced by other techniques (e.g., molecular).

Unfortunately, conclusions from different methods often conflict with each other. For example, Huelsenbeck and Hillis (1993) contrasted the success of 16 methods (including parsimony) in resolving a series of four-taxon trees with varying relative branch lengths. Four-taxon unrooted trees have the advantage of a scope of only three topologies, so it is possible to calculate simply the proportion of correct trees. The reader should see the article for the details, which I will not report here. Overall, parsimony, along with two other methods, performed well except in the case in which evolution was strongly uneven among branches and when the internodes were short, relative to the external branches. It becomes hard to resolve phylogenies when internodes are short, especially when substitutions are accumulating at very different rates in different branches. This is an extremely important result, as it may apply in cases of evolutionary radiations. In many cases, the showing of all algorithms was poor.

Is the poor showing of Huelsenbeck and Hillis the final word? This has not proven to be the case. It might be argued that four-taxon analyses are a worst-case scenario, because the addition of taxa might provide more information that would resolve cases of homoplasy for certain characters. For example, if a case of homoplasy arises in a character in a four-taxon tree, the likelihood of producing an incorrect conclusion increases, unless one has very large numbers of characters. But if one evaluates a tree with larger number of taxa, then several taxa in a monophyletic group might provide character data that will confirm the monophyly and correct cladistic position of that group.

Hillis (1996) demonstrated that surprising accuracy can be realized from data sets of hundreds of taxa. He used a molecular data set for the angiosperms to determine a tree using parsimony and then simulated other trees using a model of nucleotide substitution. These trees were surprisingly accurate, even with DNA sequences of a few thousand sites.

In most parsimony analyses, characters are all treated equally. Some have advocated *character weighting,* where some characters are assigned more importance than others, which might have more occurrences of homoplasy. Farris (1969) argued that cladistically unreliable characters could be hierarchically correlated only by chance, and supported an iterative algorithm, in which so-called cladistically reliable characters would be successively weighted, followed by a recalculation of a tree based on parsimony. Systematic cases of convergence also argue for the weighting of characters. Mitochondrial nucleotide analyses place the lancelet *Branchiostoma floridae* in a phylogenetic position that is completely at variance with our understanding of deuterostome phylogeny. This apparently results from convergence in base composition among some of the taxa, which obscures the weak phylogenetic signal in the set of deuterostome taxa. The lancelet is thus placed in a position ancestral to the echinoderms, relative to the vertebrates, even though the mitochondrial DNA database includes over 12,000 sites! Exclusive consideration of potentially nonconvergent amino acids produced what we presume to be the correct relationships (Naylor and Brown 1998).

Total evidence or analysis of congruence of molecular and morphological character sets? Owing to the revolution in acquisition of nucleotide sequences, it is commonplace to have data sets with both morphological and molecular data. For some techniques, like maximum likelihood, we cannot combine these data into a single analysis, as there is no single model that embraces the total data set. Indeed, some have argued that it might be best, in all analyses, to consider different types of data separately and then to combine the "best" of both sources of information. Not so carefully hidden in these arguments is a disdain for morphological data. Nucleotide data are thought to be superior by virtue of numbers alone; after all, we often can get thousands of sites each with 4 character states. Even a good morphological data set is likely to have no more than 100 characters, each with a few states. Because many morphological traits represent continuous measurements (e.g., body size, claw length), it is not clear how or whether to convert them to discontinuous characters suitable for phylogenetic analysis. If an inspection of trees from both data types yields a conflict, a choice of the "better analysis" will likely be biased in favor of the molecular data set. It is not always clear that molecular data are inherently superior. Rapid evolution at sites with only 4 character states makes for multiple hits (i.e., homoplasy) and difficulties in alignment of sequences, especially when additions and deletions occur.

An alternative approach to choosing the "best data set" is to extract a tree from the combination of two or more different data sets. Minimally, this process might allow us to focus on the incongruities between data sets, which would lead to questions about the reliability of given characters (Bremer 1996). For example, a positively goofy cladogram that does not square with all sources of evidence and common sense might be reckoned to derive from a poor molecular alignment. This sort of reasoning, of course, can apply only when we have reasonable expectations of the cladistic relationship in the first place.

There are three basic approaches to extracting an answer from different data sets:

1. Calculate trees from the data sets separately. Then take a qualitative look to see what differences appear, or feel more confident if the two trees are congruent.
2. Calculate trees from the data sets separately, then calculate a *consensus tree,* which is a tree that contains the minimal set of monophyletic groups that can be supported by both trees.
3. Combine the data at the outset, creating a *total evidence* data set, and calculate a tree.

The reckoning of two separate data sets (Figure 2.9) produces separate analyses for two individual data sets, and a consensus tree might be the minimal representation of evolutionary relationships supported by the evidence. A *consensus tree* extracts the parts of two other trees that are in agreement, even if they may present some apparent contradictions (Adams 1972; Swofford 1991). Consensus trees inevitably produce degradation of bifurcating nodes to multifurcations, or stars. This is not an improvement so much as an admission of uncertainty. Cases have been found (Figure 2.9), moreover, in which the total data set produces more resolution and a tree that is clearly more informative and correct than the consensus of two trees representing different data types (Barrett et al. 1991; Eernisse and Kluge 1993). Whether this can be generalized to larger numbers of informative characters is unclear.

It is as yet unclear whether considering total evidence and taking it as the "answer" is very much superior to comparison of individual data sets in order to search for incongruities. But intuitively, it makes sense that more information will be extracted from a single analysis of the total evidence as opposed to extracting consensus trees from multiple data sets. Construction of consensus trees tends to

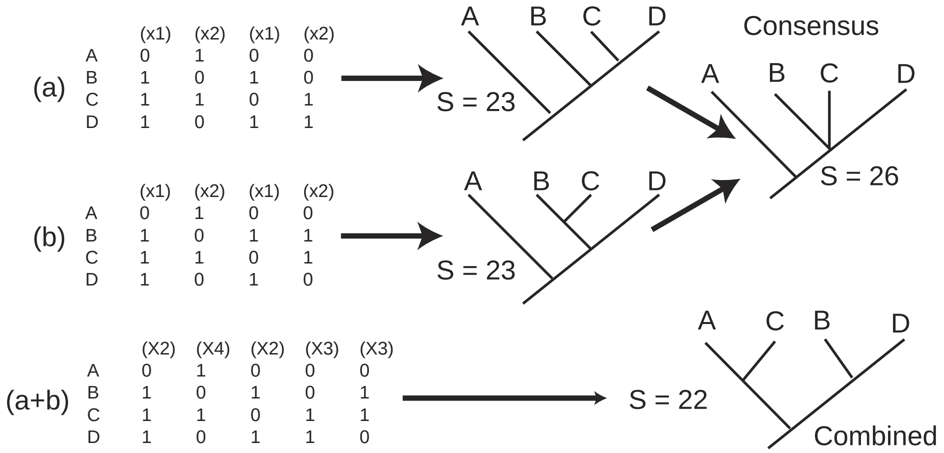


Figure 2.9. Consensus can be misleading. Characters and cladograms for hypothetical data sets A and B lead to consensus, but the total data set C leads to a combined cladogram that is four steps shorter and recovers sister group AC, which cannot be recovered by the other cladograms, which are derived from individual evidence data sets. S = the number of evolutionary steps required to produce the cladogram. (After Eernisse and Kluge 1993.)

degrade signal, especially when you consider that one is combining trees with inherently less information in each, relative to the total evidence. The consensus tree is, in effect, a lousy compromise between data sets with limited scope.

Cladists, following their version of a Popperian approach, have argued that refutation is the most efficient means of testing hypotheses. In this context, a statement describing the combined results of multiple tests is a more severe test than looking at individual components, owing to the lower probability of the intersection of combined information in scrutinizing a hypothesis (Kluge 1997). In other words, it is more of a challenge to refute a hypothesis that scrutinizes more data. In essence, total evidence should allow us to construct the least refuted hypothesis. Bremer (1996) argued that total evidence is a restatement of the principle of parsimony.

One might argue that total evidence has the extreme disadvantage of combining data sets that are inherently different and irreconcilable in terms of character states. How can a given character state derived from morphology equate to a nucleotide, which is consistently definable and has obviously homologous (alignable) sites? But consider the qualitative differences among sites or morphological characters. The 18S rRNA sequences contain distinct modes of variability, depending upon the location in the stretch of DNA (Abouheif, Zardoya, and Meyer 1998). Within morphological data sets, we may be including larval skeletal characters, adult physiological characters, and geomorphic morphometric characters, all coded in very different ways. We have no reason at present to believe that combinations of morphological and nucleotide character sets will produce any more peculiar results than analyses within characters of one type (i.e., morphological or nucleotide sequence).

One does wonder about cases in the total evidence approach in which different data sets might be better analyzed by different phylogenetic algorithms (Huelsenbeck, Bull, and Cunningham 1996). What if one data set is more likely to yield a better result with a parsimony analysis, whereas another is best suited for a maximum likelihood model? It is becoming more apparent that no method is likely to work best over the whole tree topology space (Kim, Rohlf, and Sokal 1993; Siddall 1998). Would combining such individual data sets make much sense, or would we not get more insight by analyzing a given data set by the method that works best? Of course, you will disregard this argument if your philosophical belief is that one method is the best. But if you are more inclined to an empirical analysis of performance, you may object strenuously to combining data sets whose individual characteristics lead to different types of characteristic errors in estimating a tree. If two data sets are similar (e.g., similar rates and distributions of rates of evolution among characters), it might always make sense to combine them and then perform an analysis.

Practically speaking, total evidence approaches have outperformed consensus or comparative analyses of individual data sets (Bremer 1996; Eernisse and Kluge 1993; Tehler 1995; Whiting et al. 1997). But one must always worry about cases in which parsimony analyses may give very different trees with small differences in the number of steps in the trees. Littlewood, Smith, Clough, and Emson (1997) used molecular, larval, and adult morphological data to resolve the relationships among the echinoderm classes. Three trees, differing by only two steps at most, give very different topologies, except for recovering the sister-group relationship between the holothuroids and echinoids. They argue that examination of the morphological evidence alone allows for a sensible exclusion of one of the three trees. This, of course, is an argument against total evidence, but it is also directed at the major problem that parsimony faces. If we allow for statistical error, then it makes no sense to accept just the shortest tree as correct and to exclude nearly as short trees from scrutiny.

Phenetics

Phenetic approaches group taxa by their overall similarity (Felsenstein 1982; Neff and Marcus 1980; Sneath and Sokal 1973; Sokal 1986; Sokal and Sneath 1963). A matrix of taxa by character states is used to calculate a correlation (or distance) matrix among the taxa. These correlations (distances) are then employed in a grouping algorithm to construct a tree, by successive pairings, according to successively decreasing correlations (e.g., the Unweighted Pair Group Method, or UPGMA, described in Sneath and Sokal 1973). The resulting tree has the advantage of a defined root and branching topology, characterized by given levels of overall similarity (correlation), which is amenable to a hierarchical organization. The groups are defined to a degree by all of the characters under consideration in producing the clustering. A set of subgroups included within a group need not have the set of character states that uniquely define the larger group. By contrast, cladistically defined groups have the important characteristic that all subgroups have the same character states as those that define the more inclusive group, as well as some unique states of their own, which define the lower taxonomic level of the subgroups.

Although trees can be readily constructed by the UPGMA, phenetic methods can also be employed to define clusters for the sake of defining distinct groupings, such as fossil "species" (Budd and Coates 1992; Gingerich 1979). Species are defined as phenetically clustered specimens, distinct from other clusters. *Stratophenetics* has been used to merge phenetic groups between strata to define temporally separated lower level taxa. (See Smith 1994 for an excellent discussion of these approaches.)

The theory behind the original phenetic approach supposed the premise of *nonspecificity* (Sokal and Sneath 1963). Genes had sufficiently nonspecific (pleiotropic) effects across the phenotype that any large sampling of characters would reflect the genome and, therefore, would record genealogy. Different sets of characters (e.g., cephalic and pygidial in trilobites, larval and adult in moths) would therefore lead inevitably to the same classification. Incongruencies in classifications based on different suites of characters would therefore falsify the hypothesis.

Although a ferociously contentious literature exists on the relative abilities of phenetic and phylogenetic algorithms to produce more congruence among character sets (see discussion in Farris 1983; Mickevich 1978; Rohlf, Colless, and Hart 1983; Rohlf and Sokal 1981; Schuh and Farris 1981; Sokal 1983c, 1986; Wiley 1981), it is not clear that the degree of congruence of either technique is especially good in any event (Mickevich 1978, Rohlf et al. 1983). This may be because the degree of nonspecificity is very limited. Poor congruence may derive from mosaic evolution. Differential rates of evolution of different character sets within the same monophyletic group would tend to produce different phenetic groupings using the different character sets (Farris 1971). But this would also weaken results using phylogenetic systematic methods (Huelsenbeck and Hillis 1993). Figure 2.10 demonstrates how mosaic evolution could cause differential phenetic groupings based on different character sets.

Grouping by overall similarity is more likely to lead to spurious conclusions from the genealogical point of view. Groups that have split off in the distant past but have diverged little phenetically will be grouped as close relatives. By contrast, groups that have split more recently but have diverged phenetically to a great degree will be grouped at a lower level of overall correlation. Farris (1971) gave the simple example of classifying birds, crocodiles, mammals, and snakes. A phenetic classification would group most closely the snakes and crocodiles, on the basis of similarity of both ancestral and derived characters. The lack of divergence between these two groups would obscure the genealogy relative to the other more phenetically divergent groups. To the degree that evolutionary rates are unequal in different branches

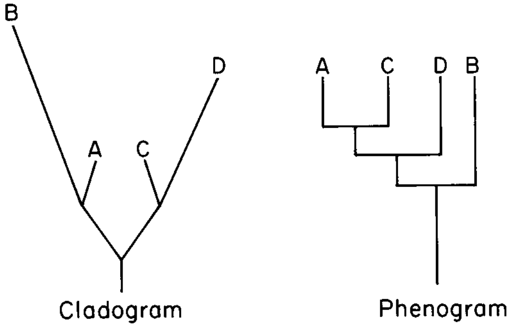


Figure 2.10. Example showing how grouping by similarity alone can be misleading in the construction of a genealogy. At left, the phylogeny is indicated, with degree of morphological divergence represented by branch lengths. At right is the grouping that would be obtained using similarity alone. (After Farris 1971.)

in a phylogeny, phenetic groupings will fail to link the genealogically closest branch points and place emphasis on the degree of phenetic divergence.

This criticism, which was Farris's fatal shot at phenetics, has come back to haunt phylogenetic approaches as well. Felsenstein (1982) pointed out that unequal rates of evolution, combined with short internal internode lengths, is an impediment to the success of phylogenetically based methods employing parsimony. This was shown in a simulation study that demonstrated a zone of chaos, where rates of change were highly unequal. Huelsenbeck and Hillis (1993) identified this type of tree topology as the "Felsenstein zone" (Figure 2.11), which hoisted Farris on his own petard. Although all phylogenetic techniques may fail under some extreme circumstances, it does turn out that the UPGMA clustering approach appears to underperform relative to other groups in recovering the correct evolutionary relationships.

Problems with phenetic clustering can be seen in Sokal's (1983a, 1983b, 1983c) comprehensive study of the caminalcules, a group of synthetic creatures whose complete history, including phylogeny, fossils, and recent species are known by definition. The phenetic classification is superposed on the phylogeny in Figure 2.12. Groups *A, B, C,* and *D,* labeled by common shading patterns, are those clustered above one arbitrary level of phenetic similarity, whereas numbered subgroups (e.g., *A1, A2*) are clustered above another arbitrary but still higher level of similarity. *B1* is the direct phyletic ancestor of *B2,* but the classification groups them as of equal rank. In another case, *C1* gives rise to *D2,* which in turn gives rise to *C4.* The *A* group is of particular interest. It includes the ancestral group, *A1,* and a derived

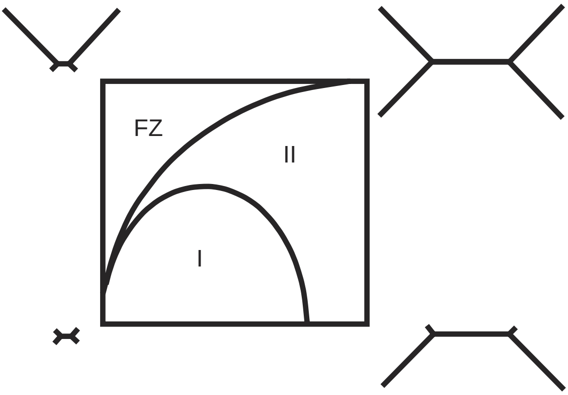


Figure 2.11. Four tree topologies of four taxa with different branch lengths. In Region I, methods such as parsimony and neighbor joining do well at recovering the correct tree, although the Unweighted Pair Group Method (UPGM) and Lake's invariant method do relatively poorly. Performance falls off in region II, where branches are long. Region FZ is the Felsenstein zone, a set of topologies that cannot be readily analyzed successfully by any algorithms to recover the correct evolutionary tree. (After Huelsenbeck and Hillis 1993.)

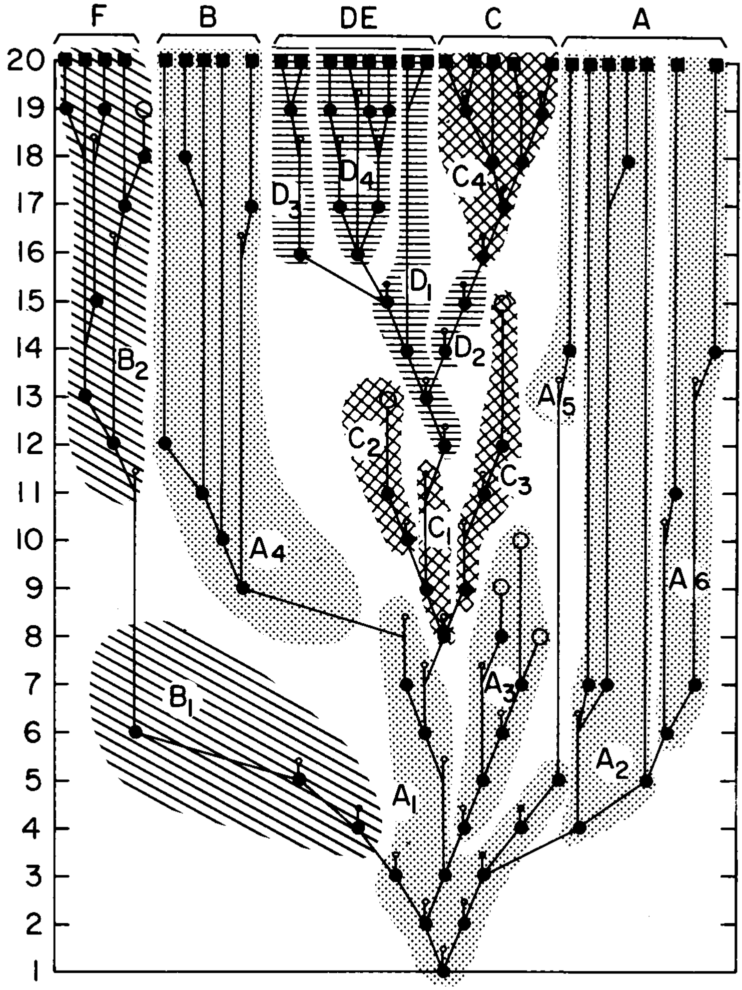


Figure 2.12. Phylogeny of the caminalcules. Shaded pattern unites group at the 0.0 phenon (similarity) level. Numbered subgroups are united at the 0.5 level. Vertical axis indicates arbitrary time units. (After Sokal 1983c.)

"radiation," *(A2, A3, A4, A5, A6)* as groups of equal rank. But *A1* on the phenogram appears to be strongly derived, whereas it is the ancestor group of the entire clade! The groupings, therefore, do not present a consistent picture as to genealogy, nor is there a way to connect the groups, given the absence of information or hypotheses on polarity of evolutionary change or derived states in common. Indeed, it is the precision of identification of defining character states in Hennigian trees that allows us to see precisely how a tree is defined. By contrast, phenetic indices amalgamate many characters into one index.

The controversy over phenetics has died because cladistic techniques have won the hearts and minds of systematists and evolutionary biologists. Overt phylogenetic approaches now dominate the pages of molecular and morphological evolution journals. Parsimony has struck most as a sensible hypothesis of evolutionary derivation, but even more importantly, most systematists have recognized the utility of identifying monophyletic groups with a system whose information can be mapped simply as character changes on a tree of evolutionary relationships. Indeed, although parsimony dominates the thinking of evolutionary biologists concerned with morphology, molecular data sets have lent themselves to other approaches that perform as well as parsimony in many cases (see the next section).

Molecular Approaches to Genealogy Construction

DNA hybridization. DNA hybridization involves hybridizing strands of DNA approximately 500 nucleotides long of an index species (whose DNA is radioactively labeled) with the DNA of a number of relatives. Heat causes the hydrogen bonds of the DNA duplexes to break down, but the sequences remain intact. The rate of dissociation of the duplexes reflects the similarity in sequence between any two test species. Repeated-sequence DNA is separated before such tests are made; the dissociation is therefore related to differences in single-copy DNA.

As it turns out, the majority of the single-copy DNA consists of noncoding genes. This would suggest that evolution is random and therefore not constrained by natural selection. As suggested by discussions in chapter 3, these sequences are just those in which clocklike divergence is possible. Indeed, data of this sort collected for birds suggest a consistency with homogeneity of rate of divergence (Sibley and Ahlquist 1983).

Distances based on DNA dissociation rates are used to make a tree by means of an *average linkage* clustering method. First, the closest pair of taxa are linked; then the next step links the taxon having the smallest average distance to the previous cluster. If the rate of molecular evolution is constant, and if this is reflected in the DNA hybridization data, then this procedure should be analogous to linkages made by Wagner trees. The two closest taxa should have the most unique shared homologies, or synapomorphies. The next closest taxon should have the next most frequent shared unique genes, and so on.

In most cases, DNA hybridization data confirm the relationships that were established previously on the basis of morphological information. This approach, however, has uncovered some striking differences, relative to our current understanding of the genealogical relationships of birds. For example, the Australian passerines appear to be far more closely related to each other than any are to relatives from other continents. A great deal of convergent evolution has masked the phylogenetic relationships to remarkable degree.

The key to the efficacy of the DNA hybridization approach lies in the truth of a molecular clock. Because the genome to be considered is largely nonfunctional, the neutral theory would suggest that the rate of change is equal to the mutation rate. Sibley and Ahlquist (1983) argue that the large number of genes involved in the technique would imply some sort of average overall mutation rate. They also appeal to Van Valen's "Red Queen" (1973b) hypothesis, which would predict random change. If, however, mutation rate varies among branches of a clade, the assumption of molecular clock can produce very misleading results. If divergence is rapid along a derived branch of the clade, the presumption of a molecular clock will lead one to presume that it had originated long ago, and the taxon would be mistakenly attached toward the root of the tree. As the variance in mutation rate among subtaxa increases, the propensity for error will increase.

Mitochondrial DNA. Mitochondrial DNA (mtDNA) has become an important tool in the study of divergence of closely related species and populations (see Avise 1994; Avise and Lansman 1983; Wilson et al. 1985). The molecule's relatively short length and ease of separation make it ideal for restriction endonuclease mapping. In vertebrates, the rate of mtDNA divergence is much higher than that of nuclear DNA, and Wilson et al. (1985) argued that this is due to the apparent inefficiency of repairing DNA damage and correcting errors of replication. Vawtor and Brown (1986) provided evidence, however, that the rate of vertebrate nuclear DNA evolution may be lower than in other groups, creating an illusion of extraordinarily high mtDNA evolution rates.

Owing to maternal inheritance, all of the mtDNA molecules in an individual are usually identical. Population bottlenecks are therefore more likely to fix rare variants than is the case for nuclear DNA. Using restriction enzyme maps, combined with sequencing of specific cloned DNA regions, it is thus possible to build up genealogies for populations and species that have diverged fairly recently. Ferris, Brown, Davidson, and Wilson (1981) estimated the age of the common mother of all chimpanzee mtDNAs at 1.9 million years ago, whereas the common mother for the mtDNAs found in common pygmy chimps lived about 1.05 million years ago. Evidence for introgression between closely related species has been found in *Drosophila* (Powell 1983). Carr, Brothers, and Wilson (1987) used restriction endonuclease cleavage maps to resolve the relationships within the genus *Xenopus*.

Direct nucleotide sequences

The sequencing revolution. The single most important change since the last edition of this book is the advent of large-scale DNA sequencing (Hillis, Huelsenbeck, and Swofford 1996); a cornucopia of organisms are now known by their nucleotide sequences as much as by their morphology. Whereas in the past, large numbers of amino acid sequences were available and were even the primary inspiration for molecular tree construction (e.g., Fitch and Margoliash 1967), they never exploded into a general-use database for the construction of genealogies. What was needed was an all-purpose technique to allow systematists to get large amounts of molecular data for the same sequence type for many related taxa.

The polymerase chain reaction (PCR) was adaptable in this way to many genes, which has made sequencing and appropriate databases accessible to many systematics laboratories. As long as there is sufficient conservatism, two short sequences of about 20 conserved nucleotides at the 5′ and 3′ end of a gene can be used to amplify DNA of a gene from a new species of population. In some cases, such sequences are "universal primers," because they permit amplification in many distantly related species, which allows totally new groups to be sequenced (Palumbi 1996). The amplified DNA can be run out on a gel, stained for nucleotides, and then either "read" by eye or run and read automatically by means of scanners or fluorochrome markers. In principle, this can yield sequences thousands of nucleotides long, although the length of a gel has until recently typically given us sequences of about 450 nucleotides per species, owing to the convenience of gel size.

We mostly have sequences from mtDNA. Ribosomal DNA (rDNA) is also especially well sampled and may be mitochondrial (12S rDNA, 16S rDNA) or nuclear (18S rDNA). The rDNA genes have interspersed stretches of highly conserved and highly variable nucleotide sequences. The former have been used effectively to construct phylogenies of phylum level relationships, whereas the latter have been used effectively in shallower divergences. Protein-coding genes, such as the mitochondrial cytochrome oxidase I, also have rich databases. Nuclear genes on the whole are harder than mitochondrial sequences to extract, but many sequences are now available. These complement an already large database of amino acid sequences. Studies such as the human genome project have greatly multiplied the speed of sequencing, and hopefully, these techniques will be applied more broadly someday to give us a sampling of genes that is phylogenetically broader in coverage than just humans and a few other species. Until now, such approaches have been mainly reserved for a small number of model species.

What can sequences do for us? Well, most important, they give us a very large number of characters. Each site has four potential character states. Transitions between the states can be studied post facto by a variety of phylogenetic techniques, but models of nucleotide evolution can be used to establish a priori models of evolution, against which sequences of various taxa can be compared. For example, mutational changes at a site between purines or pyrimidines (A,T or G,C), or *transitions,* are biochemically easier than purine–pyrimidine *transversions*. Thus, the simplest model in which all nucleotide changes are equiprobable is better substituted with one in which transversions occur at lower frequencies than transitions (Kimura 1980). Where sequences can be matched easily, this difference in rate is borne out by empirical analyses.

Are molecular data sets problematical? In many cases, the answer is yes. For one thing, homology is continually an issue in many sequences. To analyze a data set, one must have an accurate *alignment* of sequences of different taxa, so nucleotide changes can be assessed accurately. But in many cases, this can be quite difficult. In the metallothionein gene, for example, evolution is sufficiently rapid that alignment and the nature of amino acid substitutions cannot be reckoned between phyla. In 18S and 16S rDNA, alignment is a major difficulty, owing to rapid evolution and apparent insertions and deletions of interspersed stretches of sequence. Thus, uncertainty of tree reconstruction may result from alignment difficulties and homoplasy, which has hampered the analysis of larger-scale phylogenies (e.g., Eernise and Kluge 1993).

A number of methods can be used to convert DNA sequences into cladograms. All obviously depend on the degree of difference of nucleotides over the total possible number of sites. Parsimony methods (Felsenstein 1988; Fitch 1971; Swofford, Olsen, Waddell, and Hillis 1996) work analogously to the ones mentioned above, only they attempt to link taxa whose sequences require the minimum number of changes over all sites. The combination of large numbers of nucleotide sites and large numbers of taxa can make an analysis quite tedious, and many systematics laboratories may have to set aside their microcomputers for several computing days to accomplish an analysis, which still does not necessarily produce the absolute shortest tree. Computational time is the greatest when exhaustive search algorithms are employed, even though there are a number of excellent programs available for general use.

Phenetic methods of grouping such as the UPGMA can be applied to distances calculated between sequences. Distance metrics usually estimate the number of sites that are different between sequences, but there also are typically corrections for multiple hits at the same sites, uneven rates of evolution at sites, and so on. UPGMA does not work very well in producing accurate trees, but such grouping algorithms are desirable, owing to the extremely long computational times to calculate trees using parsimony, especially when the most exhaustive search algorithms are employed.

Maximum likelihood and parsimony in molecular approaches. Although parsimony can be applied to molecular data very readily, molecular data lend themselves to a completely different type of approach, *maximum likelihood,* in which a model of evolution can be used to generate approaches to selecting the most likely tree given the model (Felsenstein 1979; see also Swofford et al. 1996 for an excellent discussion). To do this, one must have the probability of evolutionary change from one state to another. In a molecular data set, for example, the transitions from one nucleotide base to another would have to be known. Given the knowledge of these probabilities, one then selects the tree with the maximum likelihood of fitting the data set, given the model. Using a few realistic assumptions, it is sometimes possible to take the maximum likelihood tree to be that which satisfies a certain criterion. For example, if the probability of evolution from an ancestral to a derived state is much higher than the probability of reversal, then the method of Camin and Sokal (1965) does very well in producing the most likely tree. This method assumes no reversals in character states.

This approach has the weakness of requiring some estimate of probabilities of evolution. The simplest case would involve the use of a homogeneous rate of evolution at all sites. But, for example, it is well known that transition nucleotide changes occur more frequently than transversions, which can be accounted by fairly simple models (Kimura 1980). Also, it is now well known that there is a considerable spectrum of rates of evolution among sites, which in molecular evolution can be accounted by a gamma distribution approximation (Yang 1993). In the case of nucleotide evolution, these corrections might work well for many point mutations (see Felsenstein 1981), but significant problems would arise in the case of frame-shift mutations. In the latter case, we could not easily assign probabilities of nucleotide transitions without knowing the specific sequence context of the mutation. Maximum likelihood has the disadvantage of computational intensity, because many trees have to be searched. In data sets of many taxa, the computational time is immense and it also may be likely that a searching algorithm will identify the wrong tree as the shortest. Nevertheless, maximum likelihood can have considerable success where other methods fail (Hillis et al. 1994), especially in the Felsenstein zone, mentioned above.

Siddall (1998) pointed out that the Felsenstein zone refers to taxa with long branches that are separated by a short interior node. But an alternative case with

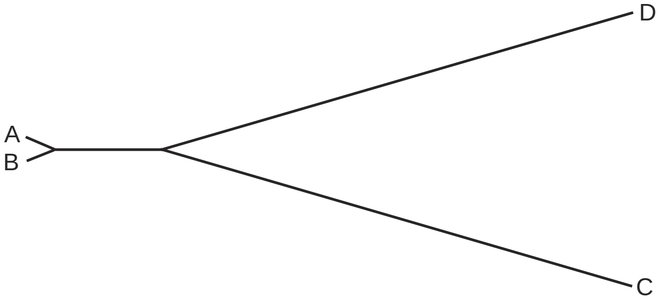


Figure 2.13. The case in four-taxon analyses where sister taxa are unusually long-branched.

four taxa can be considered where sister taxa are both long-branched (Figure 2.13). Siddall simulated a series of trees with varying pairs of rates. An unrooted four-taxon tree has five edges, so every variant had one rate for the internal edge and two adjacent terminal edges and the other rate for the remaining two edges, which were inevitably sister taxa. Parsimony generally performed best in all cases, although maximum likelihood did well in most of the simulations. Parsimony was particularly more successful than maximum likelihood in the sort of topology of Figure 2.13, where two long branches of sister taxa were connected to the other two short-branched sister taxa by a short internal edge. In effect, the long branches are repulsed in maximum likelihood analyses, the opposite of the Felsenstein zone case, where long branches are attracted in a parsimony analysis. This suggests that there may be inherent differences of success for various analytical methods in different parts of tree space. It is worth remembering that these differences occur in extreme cases, where long branches are 50 times or more longer than shorter branches. Over less extreme parts of the space, parsimony, neighbor joining (see Neighbor Joining below for description), and maximum likelihood are not terribly different in success.

Bayesian approach. An alternative method to maximum likelihood, the Bayesian approach (Rannala and Yang 1996; Yang and Rannala 1997) uses models, including a birth–death process and a Markov process of nucleotide transformation, to generate a prior distribution of phylogenetic trees; the parameters are estimated by maximum likelihood. The estimates are then used in place of the true parameters to evaluate the posterior probabilities of trees.

Neighbor joining. A number of molecular genetic distance methods[1] have been used in the past to group taxa, including those using a least squares fit of distance (Cavalli-Sforza and Edwards 1967; Fitch and Margoliash 1967; Swofford et al. 1996). Neighbor joining (Saitou and Nei 1987), however, has emerged as the most used distance-based method of tree construction. It is a clustering method that successively joins closest pairs of taxa and then removes them from the group of starting taxa, with a repeat of the process. The single tree produced is unrooted and successively clusters lineages with no subsequent rearrangements. This, in effect, contracts the distance of

[1] See Swofford et al. (1996) for a complete accounting of this subject.

taxa that are distant from the centroid of taxa and expands the distance of taxa near the centroid of all taxa, which homogenizes unequal rates of change. The method therefore does not assume homogeneous rates throughout the tree.

Compared with parsimony calculations, neighbor joining saves a tremendous amount of computational time, as its speed is inversely proportional to the square of the number of taxa, which is far better than for parsimony or maximum likelihood. Its accuracy in capturing simulated trees is not terribly different from parsimony, at least when the variance in branch length and the degree of character change are both limited (Huelsenbeck and Hillis 1993). Parsimony, however, is capable of recovering correct trees with fewer nucleotides; a study of four-taxon trees with equal rates of divergence along the branches demonstrated that parsimony could recover correct trees with near certainty with only 300 to 500 nucleotides, whereas neighbor joining required about 1,000 to get over 95% accuracy (Hillis et al. 1994). Given our current ability to acquire data, this is not a major limitation for neighbor joining, however. If you want 99% accuracy with neighbor joining, the four-taxon trees required better than 5,000 nucleotides. With strongly uneven rates of taxa distant on a tree (i.e., the Felsenstein zone), neighbor joining and parsimony converged on random or even incorrect solutions. Only maximum likelihood was capable of recovering correct trees, but only with large amounts of sequence data and very long computation times (Hillis et al. 1994).

Gene order. Gene order on a chromosome or mtDNA may be highly conserved, and changes in order may therefore be useful in determining evolutionary relationships. Along with sequences and morphological data, it has been useful in resolving higher level relationships in the Echinodermata (Smith 1992). The gene order of chloroplast DNA contains an inversion in bryophytes, when compared with tracheophytes. Characterization of tracheophyte chloroplast DNAs (cpDNAs) shows that lycopsids share the gene order with bryophytes, whereas all other vascular plants share the inverted gene order, which supports the deep phylogenetic separation of lycopsids and marks an ancient evolutionary split in early vascular land plants (Raubeson and Jansen 1992).

General Features and Problems in Tree Construction

It is appropriate here to summarize the problems in reconstructing phylogenetic trees:

1. *Homoplasy.* All characters do not produce concordant trees, owing to character reversals on scattered parts of the tree, evolutionary convergence of character states on different parts of the tree, or repeated independent origins of character states on scattered parts of a tree.
2. *Rate of evolution:* The faster the rate of evolution, the more likely it is that information for specific characters will be blurred, thus reducing resolution of a tree. This is most easily seen in molecular data, where the same site will change again and again if the rate of evolution is fast. Because there are at best only four nucleotide choices at a site, the loss of information with increasing evolutionary rate is obvious. Rates of change may also be heterogeneous over time. Older divergences appear to suggest that rates of molecular evolution for a gene are slower

than from recent divergences. This apparent difference may relate to saturation of sites after a period, making older divergence measures subject to error, owing to multiple changes at a site.

3. *Difficulty of resolving ancient nodes:* As time passes, the chance for a character to reverse or continue to change increases. Thus, ancient splits in a phylogeny should be more difficult to resolve. This problem can be ameliorated if there are characters that evolve slowly. Homoplasy is especially a problem here; where the evolutionary signal is weak, relative to multiple hits (in molecular studies), convergence and parallel evolution both help to smudge the phylogenetic signal.
4. *Long-branch problems:* If two rapidly evolving but distantly related taxa are connected by a split, they will differ by many characters. These two taxa will tend to be grouped together by numerical algorithms (Hendy and Penny 1989), and parsimony often converges on the wrong answer (Hillis et al. 1994). Errors also occur when two sister taxa have extraordinarily long branches relative to internodes and other terminal branches, especially in maximum likelihood analyses (Siddall 1998).
5. *Taxon sampling:* As one has fewer and fewer taxa, it becomes quantitatively more and more difficult to resolve monophyletic groups near the tips of a phylogeny (Rannala, Huelsenbeck, Yang, and Nielsen 1998).
6. There is no perfect technique that works best under all conditions. Algorithms that work well under some conditions may work poorly under others. Thus, for example, parsimony does well under conditions of relatively slow evolution and homogeneous branch lengths, whereas maximum likelihood tends to do better in cases of faster evolution and uneven branch lengths of distantly related taxa.

The Evolutionist–Phylogeneticist Conflict and Classification

Phylogenetic systematic practice requires the conversion of a cladogram into a classification. Hennig (1966) realized that the cladistic system would raise conflicts with other types of classifications. First, branch points in the cladogram are delineators of successively inclusive (increasingly higher ranking) groups as we move toward the root. All subgroups of a group have the same character states that define the more inclusive group, unless recognized reversals have occurred. Any two sister groups are defined by the corresponding two descendant groups found "upstream" of the tree from a bifurcation. This form of classification insists that only *monophyletic groups,* defined as all of the descendants of a single ancestral species, be recognized. It excludes the recognition of *paraphyletic groups* – groups that include an ancestor but not all of the descendants. The objection to paraphyletic groups stems from their definition by shared ancestral characters. In many cases, this set of characters fails to define the group under consideration, as other related groups also share the ancestral character states (e.g., Farris 1979).

Paraphyletic groups may preclude our ability to recover the cladogram. Consider the relationships among birds, crocodiles, and other reptiles. The group [crocodiles, other reptiles] is ambiguous, as it is a paraphyletic group bound by symplesiomorphies, or shared ancestral characters. The states uniting this group are also characteristic of the entire Amniota. The nuculid and solemyid bivalves are united on the basis of an ancestral gill, which would also define a group larger than the class Bivalvia! This hardly gives precision to the defined group Protobranchia. Yet, by describing taxon A as "strongly divergent" and referring it consistently to a cladogram, phenetic divergence information might be retained. Wiley (1981) discussed various systems, describing degrees of divergence, to annotate classifications.

The objections to the implications of the Hennigian system have mainly come from *evolutionary systematists* (e.g., Mayr 1969; Simpson 1961, 1975) whose objectives overlap only partially with phylogenetic systematists. Although evolutionary systematics aspires to produce a classification based on monophyletic groupings, the rankings of taxa are not based exclusively on position in a tree. Increasing degree of phenotypic difference from related taxa and numbers of species in a taxon both are used as criteria to raise a taxon to a higher rank, which may create paraphyletic groups, as the group most closely related to the divergent group is defined inevitably by ancestral – not derived – features (see Farris 1975).

Before pressing on to the more arcane aspects of defining classifications by cladistic logic, I want to emphasize the main principle that is at stake here with regard to macroevolution. Nearly all current macroevolutionary studies of changes in diversity use the traditional database of systematics, which uses a taxonomic hierarchy composed of a mixture of paraphyletic and monophyletic groups. As we shall discuss further in chapter 7, this taxic approach may obscure some appearances and extinctions of monophyletic groups, which calls into question a practice from which many conclusions about macroevolution derive.

Evolutionary systematists have also objected to the Hennigian classification system, owing to the effect of the addition of newly discovered taxa to an existing classification, which, of course, must add still more branch points. The discovery of new taxa would lead to continual revisions of classifications. The instability thus created becomes more worrisome as the added branch points are closer to the root and therefore define more and more higher taxa. This is particularly true of newly discovered fossils bearing ancestral characters. As Mayr (1974) noted, the "discovery" of the birds immediately defines a synapomorphy with crocodiles, making the other reptiles more distantly related and increasing the overall taxonomic rank of the group [(birds, crocodiles)(other reptiles)]. Using ancestral plus derived states, birds are more divergent phenotypically from [crocodiles, other reptiles] than either of the two reptile groups is to the other. It therefore seems intuitively reasonable to separate the birds off in a rank equal to the crocodiles plus other reptiles (e.g., Michener 1978).

Apparent progressive sequences create the most problems because evolutionary systematists wish to recognize grades of evolution by equal ranks, whereas the Hennigian system seems to require that more "advanced" groups be of lower rank. For example, evolutionary systematists would accept the equal ranking of pelycosaurs, therapsids, and mammals, because it is believed that the mammals, even though derived within the therapsids, are an important new grade of organization, which permitted an extensive evolutionary radiation. Again, as long as the cladal structure is preserved explicitly, one does not necessarily sacrifice any information. This issue lies at the heart of the analysis of fossil data, particularly that of taxonomic survivorship and longevity studies (e.g., Levinton 1974; Raup 1978; Van Valen 1973b). Such analyses would lose important information, if the classification obeyed Hennigian principles, because an analysis of taxonomic longevity will have ecological meaning only if ecologically equivalent groups are contrasted (Van Valen 1984). To make the birds subordinate to the reptiles, for example, masks their possibly equal importance in ecological effects within natural communities, degree of geographic coverage, similar number of species, and so on. Thus, current studies of taxonomic survivorship or diversity at, say, the family level, could benefit from the retention of the evolutionary systematists' frame of reference, as long as it does not obfuscate the genealogy.

As shown by Figure 2.14, progressive sequences yield asymmetrical trees that resemble combs, which emphasize the classification problems mentioned above. Groupings of one taxon with large numbers of others are inevitable, with the sister group criterion. Thus, taxon A would be of equal rank with the taxon grouping [B,C,D,E,F]. Hennig (1966) adhered to this requirement strictly, whereas others complain about redundant taxa; that is, one taxon is monotypic at several rank levels (in Figure 2.14, A is monotypic at five ranks, B at four, etc.). This problem can be solved readily (e.g., Schuh 1976; Wiley 1981). Monophyly is the only essential requirement for a consistent cladistic classification. It should be possible to retrieve the cladogram from the classification; preferably, redundant taxa should be minimized. Schuh (1976) solved this problem for the hemipteran family Miridae. All of the taxa are arrayed in a linear pattern of branching, as in Figure 2.14, which would imply a phyletic evolutionary sequence if synapomorphies along the tree are based on progressive changes of the same characters. All taxa are given equal rank, but the order of the list implies the distance along the main branch toward the taxa with the most derived states. Any listing that can retrieve the cladogram is acceptable; this leads to considerable flexibility in ranking. A proposed cladogram for the mammals (see chapter 6) deals similarly with such cladograms.

The potential problem posed by ranking according to degree of phenotypic divergence, or gaps, can be seen in Figure 2.15. Here, group [C,D] is defined on the basis

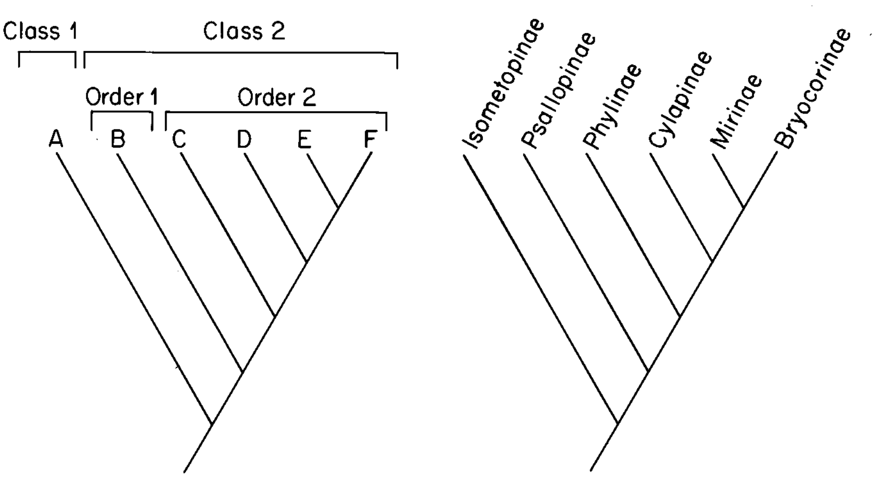


Figure 2.14. Two possible classifications that retain the genealogical information of the cladogram. On the left is a classification derived from a cladogram of six taxa. On the right is a classification of the hemipteran family Miridae (after Schuh 1976), with all taxa given the same rank.

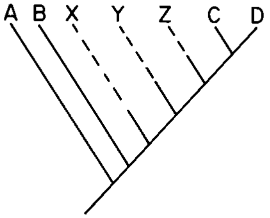


Figure 2.15. A cladogram where group [C,D] is phenetically divergent from the closest living relatives [A,B]. Taxa X, Y, and Z are hypothetical newly discovered fossils that span the gap.

of a phenotypic difference between it and [A,B]. But what if fossil intermediates X, Y, and Z are found? The reason for the gap suddenly disappears. The use of gaps thus imposes an instability on the definition of rank. This problem is only exacerbated when examining the fossil record. Although groups notably divergent from their closest relatives are common, other taxa seem to acquire gradually that final complex of characters that gives us the total character set that defines the taxon (chapter 6). Yet we wish to say: "That is a mammal!" This can be recognized implicitly in the accepted taxonomic separation of the ancestral Mesozoic mammals from the therapsids, classed as reptiles. The use of gaps in classifications involves the use of an ecological–evolutionary model as a classificatory criterion. The origin of a highly divergent group is often associated with the movement into a major new habitat and lifestyle (Mayr 1969; Simpson 1953). The assignment of high rank to such a divergent group is a recognition of an ecological–morphological advancement. This criterion, of course, is external to the genealogical structure. This would be well and good if there were one such criterion. But what if there are others, such as mode of development? It would be best to have a system that always refers simply back to the genealogy. Without such a framework, the intent behind classifications will be ambiguous, because rank is used in so many different ways by different investigators.

Because both cladists and evolutionary systematists seek some sort of genealogically based classification, I am sure that the common goal will tend to yield more imaginative solutions to the problem of ranks. Evolutionary systematics recognizes that monophyletic groups will be defined by certain sets of characters, but these characters will vary from group to group and can be discovered only by some sort of character analysis (e.g., Mayr 1969). This conclusion is close to the cladistic approach. We can see more fundamental issues in common between cladists and evolutionary systematists than differences, even though the two camps usually seem to attempt to accentuate the intellectual gaps. The present trend in systematics, designed to reflect phylogeny in classifications, is healthy, no matter what the particular approach. In many respects, it is rather useful that a plurality of phylogenetic approaches be maintained to help sharpen our understanding of evolutionary classification.

Before the era of evolutionary systematics, taxonomists tended to employ *restrictive monothetic* criteria, where specific characters were used to define differences at a given taxonomic level (e.g., internal characters define only ordinal-level differences in brachiopods). In these idealistic classifications, restrictive monotheticism implied that key characters defined given taxonomic levels (see Mayr 1969 for discussion). This approach, still an integral part of many existing classifications, derives originally from Cuvier's notion of subordination of characters, which on the one hand saw organisms as perfectly integrated living functional creatures, but on the other hand saw them as defined inherently by crucial traits that defined the essences of the taxa. This is well illustrated by the brachiopods, where certain characters were believed to define differences among genera, families, and orders (see Williams and Rowell 1965). The monothetic nature of brachiopod classifications of the late nineteenth century (e.g., Beecher 1891; Schuchert 1893) persisted into the middle of the twentieth century (e.g., Cooper 1944). Restrictive monothetic classifications often lead to the spurious uniting of groups with no genealogical significance. Newell (1965, 1969) rejected such simple attempts to classify on the basis of one criterion.

Modern evolutionary systematic approaches have departed from the restrictive monothetic system used, for example, in the brachiopods. Williams and Rowell (1965) recognized that many different characters may define evolutionary change in this group. They concluded that (p. 223)

> ...all such schemes proposed in the past are incompatible with the evolutionary history of the phylum. Previous monothetic, non-evolutionary classifications were regarded as "only catalogues ... deliberately arranged for quick identification of stocks."

The Value of the Fossil Record

The fossil record has been a surprisingly difficult subject for those wishing to construct systematic schemes and evolutionary relationships. The former is a bit easier to understand. Hennig (1966) suggested that classifications might have to ignore fossils, to avoid the problem of inserting new branches into the ancestral parts of cladograms. As new fossils were discovered, such continual regrouping would muck up Hennig's recommended systematic system, which was a hierarchically organized set of taxa consistent with the tree of evolutionary relationships. Coexistent fossils might be grouped at each time horizon, thus avoiding the problem of new branches, but this solution would create taxonomically absurd situations, such as the placement of the same taxon at different ranks, depending on its time horizon and the number of relatives (Wiley 1981). It has also been suggested that fossils be included in cladograms, but listed in classifications as extinct, with no rank. Alternatively, the fossil groups can be given a rank identical with their closest extant relative (see discussion in Farris 1976). I can't see these as viable approaches in a macroevolutionary context. We must have some consistent system for recovering the genealogies of the taxa under consideration. Fossils provide so much more information on morphology that it is ludicrous to exclude them when our resolution of understanding of transitions will be only reduced. I concur with Farris (1976) that all fossil and recent taxa should be classified together.

A deeper issue concerns the use of data from fossils and their order of appearance in the fossil record as data to reconstruct evolutionary relationships. A cloud of suspicion was raised by cladists over the utility of fossils. The value of the fossil record in systematic reconstructions has been questioned often, gently by some paleontologists (e.g., Imbrie 1957; Newell 1947, 1956; Shaw 1969) but rather strongly by others (e.g., Forey 1982; Patterson 1981). If we could trace every lineage transitionally through a perfectly preserved rock record, we might be able to use order of appearance to infer ancestral and derived taxa. But fossil sequences are often plagued by incomplete preservation, incomplete biogeographic coverage, and rapid rates of cladogenesis. Ancestor–descendant relationships can be safely deduced if a continuing nonrandom trend of change through a geological section can be established (see Raup and Crick 1981) with no evidence of cladogenesis (e.g., Malmgren and Kennett 1981; Ozawa 1975). There are also rare cases in which cladogenesis may be traced (Grabert 1959; Prothero and Lazarus 1980). Ultimately, this question can be answered only by the degree to which vertical positional information can be useful, which must vary with fossil group and time in the record.

Cases of complete ancestor–descendent records are usually those involving evolutionary transitions of small magnitude. Larger-scale transitions, such as the evolution of mammals from therapsid-like ancestors, are rarely if ever recorded in such a complete and continuous sequence (Kemp 1982). Although the morphological details of the transformation are fairly clear, specific statements concerning the exact phylogenetic pathway are best avoided. Because exact ancestors are difficult to identify, we are left with the unsatisfactory alternative of investigating the means by which one taxon could be transformed into the most closely related taxon. It follows from this argument that the only tenable way of eliminating the gap between hypothetical ancestral and derived sets of character states (e.g., the "mammalian condition" versus the "reptilian condition") is simply to find more transitional taxa! The database of available fossil and living taxa, fixed on a reliable cladistic network, is our first and foremost reference system in macroevolution. In the eruptive stages of evolutionary radiations, missing crucial data are liable to be rampant. Perhaps this is why we have such difficulty relating the phyla themselves during the Cambrian Explosion.

Completeness of the record is clearly the key to constructing an expectation for the reliability of stratigraphic order as useful data for the assessment of phylogenetic relationships of fossil groups. Some methods have been developed to assess the degree to which we can accurately estimate the ranges of taxa, and error is a function of the recovery potential of fossils and especially the size and distribution of gaps throughout a fossil species' range (Marshall 1997). In a cladistic context, consider the stratigraphic ranges of two sister taxa, whose relationships have been inferred by morphological characters alone. It is likely that the first appearance of one of the two taxa will differ from that of the other (Figure 2.16). As this gap increases, one expects that the degree of stratigraphic completeness should decrease (Benton and Hitchin 1996; Benton and Storrs, 1994, 1996). The sum of such gaps, relative to the total span of the stratigraphic record covered by all fossil taxa considered, constitutes an index of stratigraphic completeness.

Smith's (1984) analysis (Figure 2.17) of the Echinodermata stands as an exemplar of a cladistic study that unifies the genealogical relationships of fossil and extant taxa. He noted that previous classifications suffer from a lack of focus on character transformations. Using the cladistic approach, Smith produced a genealogy of the five extant classes, then added extinct groups to the cladogram. Fossils shed considerable light on certain aspects of the process. First, fossils may identify character

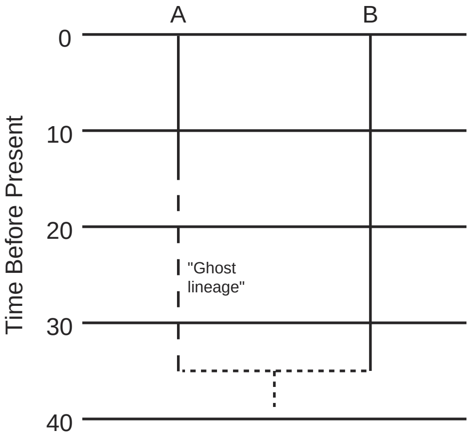


Figure 2.16. Fossil distributions of two sister taxa, A and B. If B extends to time 35, then A must extend at least to that time. The record of A therefore must be only about 43% complete.

states that may have been lost in extant groups. Second, extinct groups may reveal the pattern of character acquisition of traits that are now autapomorphic to the entire living group. This second point is crucial in understanding the morphological transformations that led to more derived body plans. We use this approach in chapter 6 to examine the origin of the mammalian condition, and in chapter 8 to revise previous notes of a Cambrian Explosion of taxa.

Some authors (Eldredge and Cracraft 1980; Patterson 1981; Schaeffer, Hecht, and Eldredge 1973) have claimed that the temporal sequence of fossils should never be used as evidence for ancestor–descendant relationships. In using the fossil record, one assumes at least that the fossil record is sufficiently complete to make a determi-

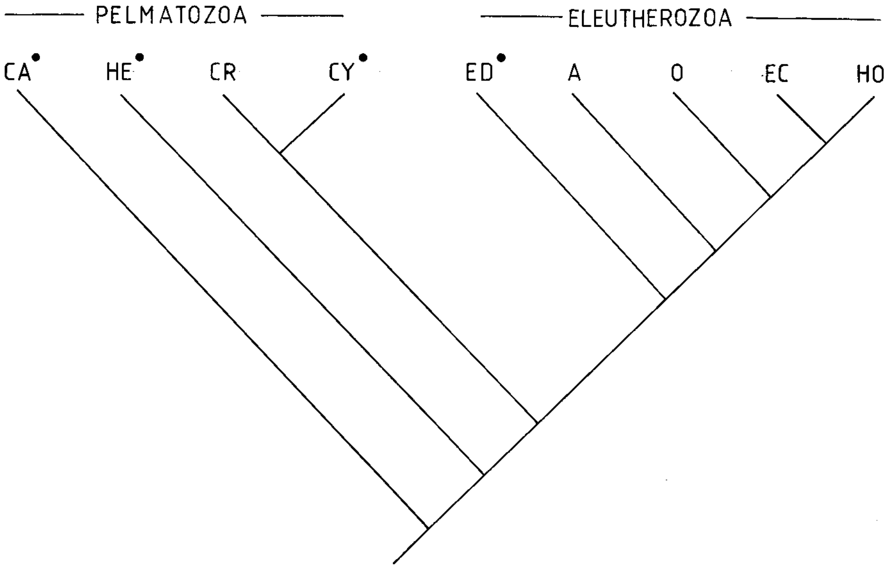


Figure 2.17. A partial cladogram of the Echinodermata, including some fossil groups. HO = Holothuroids; EC = Echinoids; O = Ophiuroids; A = Asteroids; ED = Edrioasteroids; CY = Cystoids; CR = Crinoids; HE = Helicoplacoids; CA = Carpoids. • = extinct (after Smith 1984).

nation of character–state polarity, or, at most, that younger fossils are more derived than older ones and ancestry can therefore be established. Because we know that ancient groups often survive along with their descendants, or at least descendants of the ancient groups' close relatives, the latter assumption is often false. The existence of the living fossils *Neopilina* and *Latimeria* argues against the infallibility of stratigraphic position as an indicator of ancestor–descendant relationships. One can even imagine hypothetical cases in which the fossil occurrence of a given descendant taxon antedates its ancestors, because the latter group is missing from a portion of the fossil record (Eldredge and Cracraft 1980). The closer the origins of the two taxa and the longer the period of coexistence, the higher is the probability that sequence can be misinterpreted. This is not true, however, for direct phyletic sequences. If a descendant derives by transformation from an ancestor, it is highly probable that stratigraphic sequence indicates polarity (Paul 1982). The probability of two randomly collected specimens being preserved in the wrong order cannot be greater than one half.

The strong limitations of temporal fossil occurrence in evolutionary reconstruction are especially clear when paleontologists search for the ancestor of a large taxonomic group. For example, the bivalves *Babinka* (McAlester 1965) and *Fordilla troyensis* (Pojeta, Runnegar, and Kriz 1973) have both been cited as transitional forms, which are ancestral to the mollusk class Bivalvia. In both cases, early stratigraphic occurrence is a principal part of the argument, though morphology also plays a role.

In the case of *Babinka,* a series of muscle scars were linked with the hypothetical ancestral states of the commonly cited likeness of *Neopilina* to the hypothetical ancestral mollusk (McAlester 1965). The anatomical claim was refuted by showing that the pedal muscle scar pattern in *Babinka* was not homologous to the serially repeated pedal muscle scars in *Neopilina* (see Stanley 1972, p. 166). The repeated "gill muscle scars" in *Babinka* most probably did not represent a transitional change between ancestors and later bivalves, where a single pair remains. Note that although the claim for ancestry depended on both stratigraphic position and character states, the refutation was based on an analysis of character states alone.

The case of *Fordilla troyensis* is more illuminating. This remarkable fossil is widespread in the Lower Cambrian rocks of North America and can also be found in the same Series in Denmark and perhaps England, Portugal, and Siberia (Pojeta and Runnegar 1974). Because nearly all of the bivalve superclasses were not found in rocks older than Middle Ordovician time, and only the Palaeotaxodonta appear in the Early Ordovician, *Fordilla* deserved its status in 1973 as the most ancient fossil bivalve yet discovered. There was a gap of some 40 million years between it and the beginning of the known Early Ordovician geographically widespread bivalve occurrences.

The unique fossil finds in New York State (Pojeta et al. 1973) permit reconstruction of internal scars, which have been used to establish its likely bivalve molluscan status. Individuals of the species appeared to have elongate, subequal adductors and a broadly inserted pallial line. The shape of the shell and position of muscle scars suggest a shallow-burrowing suspension feeder. These features were used by Pojeta and Runnegar (1974) to make a case for direct ancestry of the Bivalvia, via the group of Ordovician heteroconch families best represented by the Cycloconchidae. After speculating on the genealogical relationships between this group of families and the other bivalves, a tenuous link was even claimed between *Fordilla* and the univalved Cambrian rostroconchs.

The problem with this sort of reasoning is obvious. What if another lower Cambrian bivalve is discovered that harbors a set of character states completely different from *Fordilla*? Because the molluscan affinities of *Fordilla troyensis* were only recently appreciated (Pojeta et al. 1973), one can safely expect that some other group, now known too poorly to rise from the ranks of *incertae cedis,* will materialize soon as a competing ancestor. The preemptive claim made by Pojeta for this genus was based solely on stratigraphic position. There was no reason to believe, from *any* other evidence other than stratigraphic occurrence, that the character states borne by *Fordilla troyensis* were necessarily ancestral. There might have been a large and diverse bivalve fauna in Early Cambrian time that has gone unnoticed or unpreserved. This is not outlandish, given the 40-million-year span between *Fordilla* and later bivalve occurrences.

As it turns out, another, still older, bivalve mollusk was discovered in Early Cambrian rocks of South Australia by Peter Jell (1980) and was reverently named *Pojetaia runnegari* (Figure 2.18). A later morphological analysis with well-preserved specimens (Runnegar and Bentley 1983) established clear similarities between this form and the Palaeotaxodonta, a group often thought to be an ancestral bivalve subclass. This discovery only emphasizes the great potential for further discoveries in Early Cambrian rocks and the dangers of searching for ancestors by means of stratigraphic position.

This example is unfair, perhaps, as an indictment of the use of stratigraphic order to infer phylogenetic relationships. After all, the inferences here were clouded by poor preservation and the general difficulties of inferring relationships in the Cambrian, the time perhaps when the bivalve groups were beginning to diverge.

The study of evolutionary transitions between the fishes and the tetrapods has been similarly influenced by the fossil record and by overall similarity between puta-

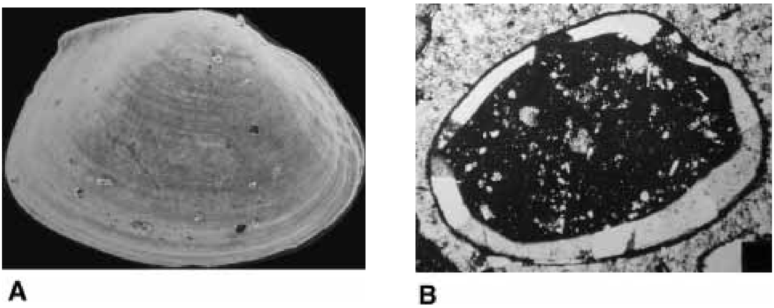


Figure 2.18. A bivalve from the Early Cambrian of South Australia. (**A**) *Pojetaia runnegari,* phosphatic coat of right valve; (**B**) *P. runnegari,* near-sagittal section. (From Bengtson et al. 1990, with permission.)

tive ancestors and the descendant tetrapods. The Rhipidistia have been traditionally thought to be the tetrapod ancestors, on the basis of overall similarity in the skull roof, appendages, and appropriate stratigraphic position. In particular, the presence of paired internal nostrils (choanae) has been cited as a linking character. Rosen, Forey, Gardiner, and Patterson (1981) claimed that the interpretation of this character is incorrect and that the rhipidistian *Eusthenopteron* lacks choanae. By contrast, a restudy of a Devonian lungfish from Australia suggests the presence of choanae. Thus, the restudy of characters placed the Dipnoi (lungfish) as the sister group of the tetrapods and completely changed our conception of vertebrate phylogeny. Rosen et al. noted that overall similarity and the connection by stratigraphic proximity led us astray. Whether this interpretation is correct or not, it places the onus on paleontologists to avoid stratigraphic assessments of ancestry and classifications based on overall similarity, which might involve grouping with ancestral characters.

Ancestors aside, temporal sequence in fossil occurrence provides useful genealogical information (Fortey and Jefferies 1982; Harper 1976; Paul 1982). In some cases, as noted above, closely spaced samples reveal a gradational sequence of morphological change from ancestor to descendant, with no evidence of cladogenesis. Although one can never exclude the possibility of something happening "between the lines," such studies, common in deep-oceanic sediments in groups such as foraminifera (e.g., Bettenstaedt 1962; Grabert 1959; Malmgren and Kennett 1981), can rightfully justify temporal sequence as evidence for character polarity.

Temporal sequence may be a corroborative tool to strengthen a hypothesis of genealogy (Eldredge and Cracraft 1980, p. 58; Miyazaki and Mickevich 1982). Consider the following analysis. A systematist establishes a cladogram, which is rooted on the basis of an outgroup comparison or by an assumption of character state polarity using ontogenetic change. This analysis yields a cladogram showing an array of taxa that can be arranged from near the most ancestral state to most derived. If the stratigraphic order of the taxa occurs in the order "predicted" by the cladistic analysis, then the conclusion of character polarity based on character analysis alone is strengthened.

An example of this sort comes from the work of Miyazaki (Miyazaki and Mickevich 1982) on the evolution of the Miocene–Pliocene scallop genus, *Chesapecten,* preserved in basins in the eastern coastal plain of the United States. On the basis of ontogenetic change, the cladogram in Figure 2.19 infers a genealogy and roots the tree near the taxon with the most "juvenile" features as an adult. The cladogram is closely concordant with stratigraphic order. The cladogram and stratigraphic occurrence data can be properly considered as independent sources of evidence leading to a similar conclusion of descent.

Temporal sequence may also resolve vexing cases of convergence when other approaches fail. The two Cenozoic radiations of planktonic foraminifera demonstrate the difficulty of identifying particular morphs without good stratigraphic information (Cifelli 1969). A Paleocene radiation from globigerinid ancestors resulted in a morphologically diverse array of taxa, nearly all of which disappeared by the Oligocene. A second radiation in the Oligocene–Miocene repeated many of the species in such faithful similarity to those in the first radiation that a proper systematic assignment is impossible without the appropriate stratigraphic information.

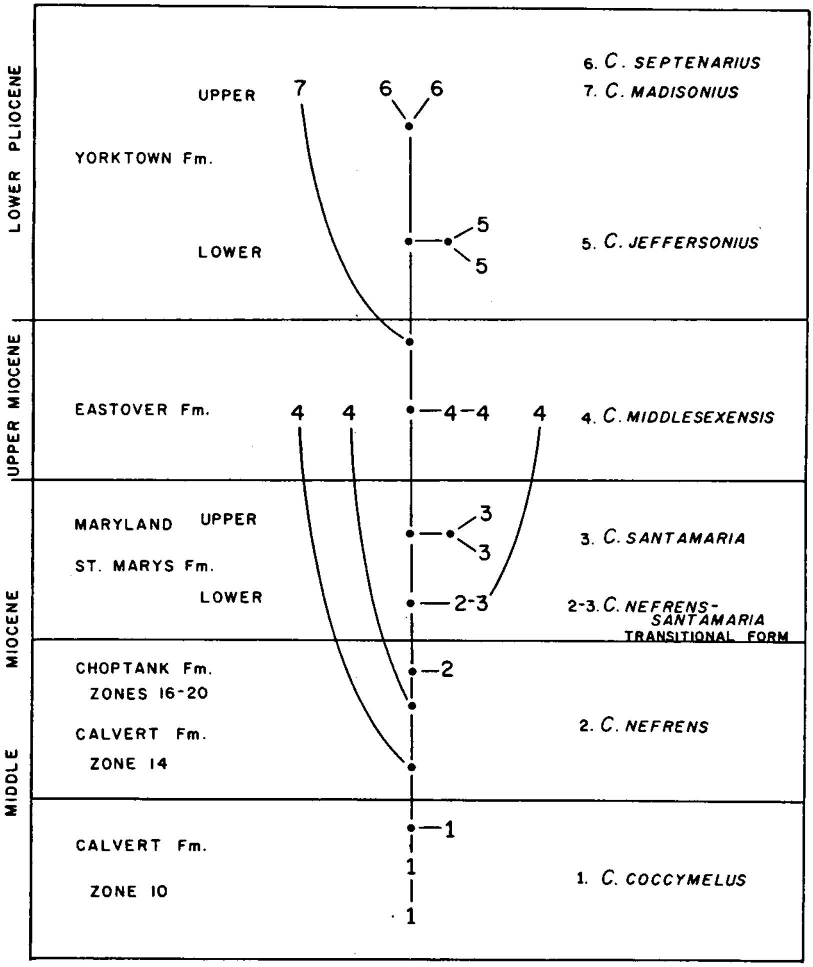


Figure 2.19. Cladogram for the Miocene–Pliocene Atlantic coastal plain scallop *Chesapecten,* superposed on the stratigraphic sequence. (From Miyazaki and Mickevich 1982, with permission.)

Stratigraphic and paleogeographic position may also be used to a degree to resolve problems in character reversal and parallel evolution. In some cases, identical derived character states may be acquired independently within several monophyletic groups, when independent stratigraphic and geographic evidence isolates these groups from each other. In the ancestral trigoniacean bivalves, stratigraphic position is essential in genealogical reconstructions (Newell and Boyd 1975). The hypothesis that parallel evolution has occurred produces the most corroborated hypothesis of genealogy. Although one can only speculate on the cause of such parallelism, commonality of ground plans might result in a similar response of independent groups to an environmental change. In any case, this approach parallels the use of gene duplication events (e.g., Goodman et al. 1982) as likely devices to increase the consistency of molecular evolutionary lineages.

It might be argued that forams and mollusks are so simple that constraints will often lead to parallel or iterative evolution. One might expect repeated morphologies here but not in higher organisms such as mammals. The widespread occurrence of atavistic character states in vertebrates (e.g., Riedl 1978) makes this claim highly unlikely. In vertebrate jaws, developmental fields can be defined where correlations among characters are stronger than with characters in other putative fields (Kurtén 1953). Thus, ancestral character states often reappear in lineages as coordinated complexes. Consider the case of *Lynx lynx,* whose fossil record has been studied extensively (e.g., Werdelin 1981). In some Pleistocene and Recent specimens, a coordinated appearance of the *M2* molar and a postcarnassial element derives from ancestors where the condition is completely absent (Kurtén 1963). Indeed, the *M2* molar has been lost in the Felidae since the Miocene! For an unknown reason, the characters have reappeared with noticeable frequency and with sufficient morphological complexity that they can be regarded as a character reversal toward an ancestral condition.

Despite the caveats concerning the influence of errors of stratigraphic position, evolutionary radiations, and incomplete preservation, it may surprise the skeptical reader just how good stratigraphic position can be in recording correctly the order of stratigraphic relationships. The simplest test, *node–order correlation,* would be to calculate a correlation between the order of first appearances of fossil groups with the order of nodes in a cladogram, deduced from morphological data alone. To do this in a simple way, complex cladograms are usually collapsed to a pectinate form so that order of nodes in a cladogram and geological occurrence can be related directly. A test of this sort demonstrates for many groups a significant correlation between node position and order of first appearance in the fossil record (Gauthier, Kluge, and Rowe 1988; Norell and Novacek 1992a,b; Sereno et al. 1999).

Stratigraphic consistency is another and perhaps more powerful means of comparing the record of fossil appearances with the order in a cladogram (Clyde and Fisher 1997; Fisher 1994, Huelsenbeck 1994). A node in a cladogram is consistent with the rock record if the stratigraphic first occurrences of the taxa above it are younger or equal in age to the node below. Therefore, an inconsistent node has stratigraphically older taxa that are placed in more derived nodes. This comparison can be readily done with intact cladograms, which need not be reduced to pectinate form. The index is simply the number of stratigraphically consistent nodes divided by the total number of relevant nodes (the root node cannot be tested). Hitchin and Benton (1997) tested hundreds of cladograms of fossil echinoderms, fishes, and continental tetrapods and found a high degree of stratigraphic consistency for all groups, with a mode at about 0.75% consistency. Echinoderms appear to be the best. Stratigraphic consistency was well correlated with the node–order correlation measure mentioned above. Interestingly, neither the node–order correlation nor the stratigraphic consistency measures were significantly correlated with the degree of stratigraphic completeness, measured by discrepancies of first appearances of sister taxa (e.g., Benton and Hitchin 1996).

This apparent success has led to the new field of *stratocladistics*. Like conventional cladistics, stratocladistics relies on parsimony and attempts to minimize ad hoc hypotheses of homoplasy and failure of preservation of fossil lineages in intervals that contain fossils. An interesting advantage of using temporal data is the possibility of identifying ancestors and even connecting lineages of fossil taxa. As we have discussed above, cladistics logically excludes such a possibility. Stratocladistic hypotheses of relationships attempt to minimize two types of ad hoc hypotheses: homoplasy and temporal order. The former is discussed above. The latter simply involves minimizing cases in which a more ancestral taxon appears in the record after the first appearance of a derived taxon.

A simple analysis is illustrated in Figure 2.20. The phylogenetic tree on the left is consistent with the character data, but the derived taxon A "skips" two time intervals before appearing at stratigraphic level four, even though B and C are preserved in those levels (two and three). The tree on the right requires no such ad hoc hypotheses of nonpreservation, but taxon A must have two character reversals relative to its immediate ancestor, taxon B. Thus, these two trees are equivalent.

Does stratigraphic order perform significantly worse than characters in constructing a cladogram? To test this question, we need a measure that applies to both trees. Clyde and Fisher (1997) used a derivative of the retention index (Farris 1989) to compare trees from 29 published data sets, mainly from fossil vertebrates. The retention index measures the degree to which homoplasy must be invoked for a given cladogram of relationships based on parsimony. Therefore, a cladogram whose characters are completely consistent (all characters would individually produce the same tree) has a perfect index of 1.0. Clyde and Fisher (1997) compared

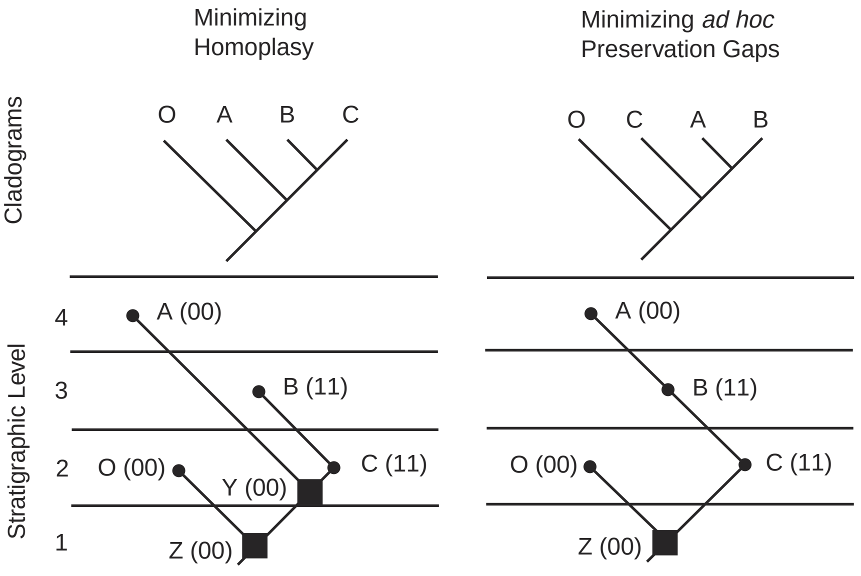


Figure 2.20. Conventional cladistic versus stratocladistic analyses. Left: Cladogram derived from fossil occurrences below, showing minimization of homoplasy. Right: Cladogram derived from minimizing ad hoc preservation hypotheses but requiring instances of character reversal. Filled boxes represent putative ancestors. (After Fox, Fisher, and Leighton 1999, with permission from the American Association for the Advancement of Science.)

the number of ad hoc statements of homoplasy required to construct a morphological tree with the number of mismatches between expected and observed stratigraphic order, assuming roughly equal probabilities of fossil preservation and recovery. We must also assume that instance of homoplasy is equivalent to one ad hoc stratigraphic hypothesis. In the absence of any clear way of scaling these two types of data, this assumption should be accepted, but perhaps with caution.

If we examine the most parsimonious cladogram derived from morphological characters (retention index = 0.80), it is clear that the stratigraphic retention index is inferior (retention index = 0.59). This would seem to settle it, but suppose we take the stratigraphically most parsimonious tree consistent with the least homoplasic tree derived from morphology. Surprisingly, the mean morphological retention index is 0.71 and the stratigraphic retention index is 0.77; these are not significantly different from each other. Further, if the stratigraphic and morphologic evidence is combined, the retention indices for stratigraphic data (mean = 0.79) does not differ statistically from the morphological retention index (mean = 0.75). With combined data, the stratigraphic data seem not to degrade the retention index, which suggests that if we take homoplasy as the main criterion of judging the efficacy of trees, stratigraphic data do not degrade the signal as argued previously (Norell and Novacek 1992a, 1992b). A large-scale simulation study demonstrated that stratocladistics could recover the correct phylogeny over twice as frequently as conventional cladistics (Fox, Fisher, and Leighton 1999).

What can we conclude from all this? First, it is clear that stratigraphic order definitely provides useful data for the construction of trees, or at least such data do not of necessity degrade the phylogenetic signal. Whether stratigraphic data will change conclusions about evolutionary relationships is not so clear, but Clyde and Fisher (1997) have now challenged us to consider the possibility that when morphological and stratigraphic data are combined, the stratigraphic signal does not blunt our inference.

The Main Points

1. A genealogy connects taxa by a criterion of relationship by means of descent. But taxa are traditionally connected by a hierarchical systematic framework that assigns successively higher ranks to deeper and more ancestral nodes. Criteria for such connections often combine phylogenetic relationships and overall resemblance.
2. Macroevolutionary hypotheses often depend on available systematic structures, as they involve such factors as changes in diversity at specific taxonomic levels (e.g., family level), taxonomic survivorship curves, and phylogenetic hypotheses.
3. The approach taken to systematics can therefore affect the meaning of macroevolutionary claims. For example, the argument that “phyla appear first in the fossil record” seems tautological, if phyla are grouped purely on the order of cladogenesis. The first splits, of necessity, would come early in biotic history. On the other hand, if phyla are organized strictly on the basis of similarity of characters, the statement might mean that some fundamental process permitted strong differences to arise early in the Phanerozoic and subsequent phylum appearance was dampened.
4. Classifications based on genealogical groupings are preferable, because it is then possible to map the character changes involved in transformations from one

taxon to its closest relative. Genealogical connections lend themselves to hypotheses that relate phylogenetic history to adaptation. Without such a grouping, the historical constraints behind evolutionary change will be missing.

5. Phylogenetic systematics overtly attempts to construct genealogical trees and to devise classification schemes that can map simply to the genealogy. Taxa are grouped by their uniquely shared derived character states. This grouping process produces strictly monophyletic taxa. Successive groupings of taxa lead to the construction of a cladogram of genealogical relationship. The cladogram can be rooted by means of an outgroup, which is ancestral relative to the group under study.
6. Character states are used to construct the cladogram, but not all characters produce congruent trees. Homoplasy occurs when different sets of characters are in conflict; this arises chiefly from errors in identifying homologous characters, partially because of convergence, and from parallel evolution in isolated lines. Several approaches have been devised to resolve incongruency due to homoplasy. The majority set of compatible characters may be used to define the cladogram. Alternatively, the tree that requires the most parsimonious evolutionary path (minimum number of evolutionary steps and reversals) is used to construct the proper genealogy. The latter approach is more effective, as it uses that information from conflicting characters that might help in resolving the tree.
7. It is crucial to identify homologous characters. Homology is a form of correspondence of characters between taxa; we hypothesize that the correspondence represents an evolutionary correspondence – that is, a space–time continuum of evolutionary change between the two characters on the two organisms. Criteria for homology mainly involve similarity of position in space and ontogenetic appearance in the organism. Except for molecular data, we rarely know the genetic correspondence for homologous characters. Indeed, there may be none for certain morphological features that are retained by natural selection, but the underlying genes may have changed.
8. Phenetics groups taxa by overall similarity. The grouping algorithms are usually straightforward, and a root arises automatically from the grouping. Phenograms have the disadvantage that specific character transformations cannot be mapped directly, because many character changes contribute to a given grouping, often in intuitively obscure ways. Phenetic groupings will probably not correspond to genealogical grouping when the rate of evolution is highly uneven through the group. Groups that have been long divergent but have slow rates of evolution will be spuriously grouped as close relatives. If the rate of evolution is fairly homogeneous for many characters, then phenetic grouping should have strong genealogical significance. This lies behind the claimed efficacy of the DNA hybridization technique.
9. Evolutionary systematics groups taxa by the two criteria of overall similarity and relationship by descent. Evolutionary systematists object to cladistic classifications, as the former wish to ascribe strong significance to strong gradational changes in evolution. The overall objectives of evolutionary systematists are not all that different from those of phylogenetic systematics. Gradational changes can be accommodated in a phylogenetic systematic approach.
10. Molecular approaches analyze sequence data to produce trees. While molecular data can in principle be analyzed like morphological data, its profusion has inspired a more open use of a variety of analytical methods to calculate trees.

Parsimony lends itself well as an optimality criterion in such analyses, but maximum likelihood approaches have also proven successful in resolving phylogenies. Distance grouping methods such as neighbor joining also produce successful phylogenies.

11. Some have claimed that fossil taxa and the fossil record are very problematic in the construction of genealogies. Although it is true that the order of first appearance can be misleading as to genealogy, the order of appearance of fossils corroborates a cladogram based on a character analysis. Fossil taxa often provide crucial links in genealogies; indeed, many character transformations could not even be imagined without fossil data. Genealogies are best constructed with the full benefit of fossil information. In recent years, order of appearance of fossil groups has been shown to be surprisingly useful in the construction of mammalian cladograms.

CHAPTER 3

Genetics, Speciation, and Transspecific Evolution

> To sum up, interspecific differences are of the same nature as intervarietal.
>
> – J. B. S. Haldane

Why Worry about Species?

Goldschmidt (1940) defined macroevolution as evolution above the species level and envisaged speciation as the crossing of a threshold of major genomic reorganization. Although his specific ideas of change are now outmoded, the mechanisms and effects of speciation are still hotly debated, and many still see speciation as a vault through the looking glass, leaping past new evolutionary thresholds. The punctuated equilibrium hypothesis, for example, is in search of a mechanism that focuses most morphological change at the time of speciation. The crux of the matter is how to relate genetic and phenotypic variation within a population to divergence between species. Are speciation and the subsequent genetic divergence merely an extrapolation of within-population variation, or is there a consistent jump in genetic and phenotypic difference? If speciation is a special time of reorganization, then the elaboration of large phenotypic differences in evolution would be enhanced both by the rate of speciation and by extinction that is selective relative to a suite of morphologies. Macroevolutionary questions place a magnifying glass on our understanding of speciation and its effects.

Our discussion can best be framed as a series of questions:

1. What are species?
2. Are the genetic differences between species of the same sort as intraspecific differences?
3. Does speciation accelerate differences important in major evolutionary change? Indeed, is that what speciation is about?
4. If the differences are significant, then does this make a difference to theories concerning the process of macroevolution?
5. Are species accidents or adaptations?

A sketch of the history of species concepts should be kept in mind as we consider these questions. Species concepts break down into a few categories:

1. Typological species concept (Linnaean)
2. Biological species concept
3. Evolutionary species concept
4. Phylogenetic species concept
5. Recognition species concept
6. Cohesive species concept

The original *typological concept* was *essentialist*; species were endowed with a platonic essence (see chapter 1). Practically speaking, philosophy does not matter, for many species can be distinguished by morphological differences, and there are examples of peoples able to nearly match the acumen of the most advanced systematist (although sibling species can't be included in this). Therefore, it is no surprise that as the issue of essentialism disappeared in the twentieth century, systematists still took the species level to be fundamental. In its new guise, it became a *morphological species concept,* which defined species typologically by key identifying characters. Although variation was not ignored, identification and distinguishing features were the foci of species. If you named a new species, you had to (and still have to) deposit a series of types in a collection and recount why this form differed from all other named species.

It was only with the advent of such works as Haldane (1932a), Dobzhansky (1937), and Mayr (1942) that the Darwinian notion of species mutability and the neo-Darwinian theories of genetic change were united into a general theory that saw species as arising from within-species variation but bound by membership in a common reproductive community. Divergence between daughter species was thought to be of the same qualitative sort as geographic divergence within species. Separation led to fixation of genes that caused incompatibilities when isolated populations again came into contact, though species were believed also to be under selection after contact for prezygotic isolating mechanisms and ecological divergence from other species (Dobzhansky 1937, Mayr 1963). Of course, the multiplication of species allows for the multiplication of independent evolutionary units that can respond in different evolutionary directions.

Reproductive isolation is the cornerstone of the *biological species concept.* "Species are groups of actually or potentially interbreeding populations that are reproductively isolated from other groups" (Mayr 1942). Note that this concept cannot, of necessity, apply to asexual organisms. More importantly, there are likely many isolated species (at least under this definition) that are reproductively compatible but do not interbreed currently, even though they may be distinctly different morphologically and genetically. Thus, the biological species concept allows for three cases:

1. Complete geographic separation of two species
2. Geographic contiguity of the geographic ranges of the two species
3. Sympatric occurrence of two species, who do not interbreed

Many of the phenotypic differences between species may not have caused, nor contribute at present, to reproductive isolation. Indeed, there is no necessary scale of phenotypic difference that we can use to define a biological species, even though there are metrics of genetic distance and phenotypic difference that, on average, predict separation at the species level reasonably well. Because there are many instances of morphologically nearly indistinguishable sibling species, we can state with authority that morphological jumps in speciation fail to occur in many species complexes. We cannot, however, readily predict that speciation will generate a given amount of morphological divergence. For example, the Tropheus lineage of the cichlid radiation in Lake Tanganyika consists of a large group of species that are morphologically nearly identical but nevertheless quite genetically divergent (Sturmbauer and Meyer 1992). This lineage of six species contains twice as much genetic variation as the entire morphologically highly diverse cichlid assemblage of Lake Malawi.

One conflict underlies many of the current arguments in both speciation theory and population genetics. Species are regarded either as exquisite adaptations or accidents of divergence. The first alternative was championed by Dobzhansky (1937), who regarded speciation as a process involving intense selection for balanced and integrated gene pools, and, therefore, against pairings among individuals from different gene pools. Part of this adaptation was achieved when two formerly isolated populations were reunited. Selection against hybridization was part of the completion of the adaptations of the two new species. The selection resulted from hybrid inferiority in either of the habitats to which the daughter species had become adapted. The biological species concept became enmeshed in the issue of selection against hybrids, especially when considering sympatric sister species. This view of adaptation to local environments and against interbreeding contrasts with that of H. J. Muller (1939), who believed that after divergence, hybrid sterility arose by chance as a product of change in the genetic background, either by drift or adaptation to different biological situations. Isolated populations moved toward "ever more pronounced immiscibility as an inevitable consequence of non-mixing."

Evolutionary or *anagenic species* are temporal successions of fossil lineages that transform one into the next with no cladogenesis. They are used commonly by paleontologists (see chapter 6) and demonstrate that significant spans of geological time often witness a succession of transitions that involve a degree of morphological difference we encounter between extant and coexisting species. The definition must of necessity be phenotypic. On the one hand, one might argue that such changes do not involve splitting and therefore the entire lineage must be classified as a single species. On the other hand, the fact that so many evolutionary species have been established and continue to be recognized is a demonstration that phenotypic changes on the order of species differences can be achieved commonly without splitting. A slight variation of this definition allows cladogenesis. Here the environment is gradually shifting and a newly evolved descendant evolves and coexists with its ancestor for a time. Then as the environment continues to shift, the descendant supplants the ancestor. In the long run, this alternative leads to a similar anagenic chain of ancestors and descendants.

The phylogenetic species concept seems to derive nicely from the biological species concept, but it instead opens a can of worms. A *phylogenetic species* is an irreducible monophyletic cluster of organisms that is diagnosably distinct from other such clusters. Thus, each species can be mapped onto a cladogram. Phylogenetic species can be regarded as the smallest monophyletic group of common ancestry (deQueiroz and Donoghue 1990). This definition can be consistent with the biological species concept, but it eschews considerations of reproductive isolation. Although Mayr's definition, quoted above, does not necessarily require anything more than a lack of interbreeding, many additional aspects of the biological species concept (e.g., reinforcement of isolation by secondary contact) are absent from the phylogenetic species concept. Indeed, it is fair to say that proponents of the phylogenetic species concept feel that cladistic status is the only means of recognizing species. Species, therefore, are recognized by synapomorphies.

The phylogenetic species concept has the advantage of consistency with evolutionary descent, but species concepts come into conflict over the issue of reproductive isolation. Consider a case in which a series of populations can be distinguished by characters, but one of the populations, the most derived, is reproductively isolated from the others (Figure 3.1). A cladistic consistency argument will immediately identify the members of species A as paraphyletic, even if derived species B is monophyletic.

This problem can be merely annoying, but things can be much worse. For one thing, phylogenetic species could readily consist of a group of populations that are currently, but ephemerally, identifiable as monophyletic groups. It may well be that all three populations of A (Figure 3.1) might introgress completely, leaving a simpler tree of A and B as terminal taxa. The phylogenetic systematics approach tends to reject such dispersal possibilities, which is probably why there is no great concern for such mixing.

As time passes, this problem will probably diminish. If stabilizing selection is very strong then alleles may be retained for long periods of time in two species that descend from a parent species. Otherwise, alleles will be lost by drift, so the probability of introgression of alleles by hybridization will decrease. In general these problems exist in the short run because trees of genes are not the same as trees of divergent taxa. The same alleles may be inherited by two daughter taxa that are

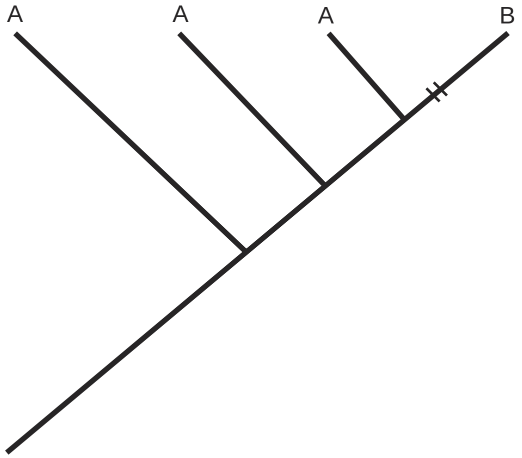


Figure 3.1. A cladogram showing population B, which is reproductively isolated from the three A populations. If the three A populations are reproductively compatible, then conflicts exist between the biological species concept and the phylogenetic species concept.

reproductively isolated, or each daughter may stochastically inherit different alleles. After a time, however, drift will result in alternative alleles being fixed in the different descendant taxa.

In the *recognition species concept,* species are the most inclusive population of individual biparental organisms that share a common fertilization system (McEvey 1993; Paterson 1985). Paterson believed that Mayr overemphasized isolating mechanisms between species. He argued that species arise as incidental consequences of adaptive evolution entailing individual selection, as opposed to species being "adaptations," having coadapted gene complexes that isolate them from other species. Isolating mechanisms would have an advantage in the zone of overlap between incipient species but not otherwise. The *cohesive species concept* (Templeton 1989) also argues for the importance of cohesive properties of species. This latter notion, however, is consistent with Dobzhansky's ideas of an integrated genotype, fashioned by natural selection, whose fitness would be lowered by cross-breeding with other closely related species.

Speciation: Process and Product

In the classic *Evolution: The Modern Synthesis* (1940), Julian Huxley defined two classes of speciation mechanisms: one associated with divergent natural selection operating on populations in separate and different habitats and the other involving genetic mechanisms (e.g., polyploidy) largely independent of adaptation and occurring more rapidly than the first. The first is a process of speciation that is essentially ecologically driven, and morphological change might be part of the speciation process itself. Genetically driven mechanisms may involve the accumulation, in isolation, of sterility genes and may or may not involve morphological differentiation. It is not clear that such a sharp distinction is useful, although the components – selection for adaptive traits and fixation of genetic differences – still loom over any discussion of speciation.

The difficulty in grasping the speciation process is understandable, as no one has ever observed it in nature, nor has anyone identified definitively what exactly happens as one species gives rise to two descendants. Instead, we can usually only observe the outcome of speciation and try to reconstruct the origins of species and the consequences of species formation. The time scale is part of the problem. The process must usually take longer than a lifetime of human observation, even if it can be geologically rapid. The renowned fish family Cichlidae has long been known to be able to produce distinct species in a few thousand years (e.g., Brooks 1950). Lake Victoria appears to have dried up 12,400 years ago, suggesting that the endemic cichlid fauna arose since then (Johnson et al. 1996). The Mbuna species flock of Lake Malawi may have diverged even more recently, owing to an episode of drying and lake lowering over several hundred years, followed by lake level rise and spread of cichlids among a large number of isolated rock outcroppings, which produced separate Mbuna faunas at nearly every outcrop area (Owen et al. 1990). The extremely slight mtDNA divergences among species suggest very recent speciation. Repeated droughts and increases of rainfall probably created numerous opportunities in rift valley lakes for the establishment of different founder populations, upon which sexual selection operated to produce new species. Even if we regard these as speciation events, we must remember that extensive genetic differentiation has not occurred in most cases, and isolation may have been driven by small-scale natural selection and sexual selection events that were indeed rapid (Galis and Metz 1998). Avise, Deette, and Johns (1998) used comparisons of minimum and maximum values inferred from genetic distances between, respectively, extant pairs of intraspecific phylogroups and sister species to conclude that speciation in many groups of vertebrates arising in the Pliocene and Pleistocene took at least two million years to complete speciation, as defined by reciprocal monophyly of gene lineages (see The Genetic Transition in Speciation). Thus, the process of reproductive isolation or ecologically significant evolution might be rapid, which is then followed by the more stately pace of establishment of more extensive genetic isolation found between typical extant sister species. Stebbins (1983a) noted that although new species of facultatively autogamous plants may arise in only a decade or two, regularly outcrossing annuals probably take hundreds of years and woody plants probably take thousands to speciate.

These time spans are unfortunately ungainly to study by either paleontologists or neontologists. For example, Williamson (1981) described a "sudden" species-level change in a snail lineage that occurred over a time span of 10,000 to 40,000 years. Cisne, Chandlee, Rabe, and Cohen (1980) described a species-level phyletic change that could be bracketed within a 200,000-year interval, but Sheldon (1987) claimed an average time resolution of about 1,000 years in an Ordovician study of trilobites, where species-level changes occurred on the apparent scale of 10^4 to 10^5 years. Although some cases of annual varves might make the study of sudden change accessible (e.g., Bell and Haglund 1982), most geological sections preclude detailed sampling even of 10,000-year units (see chapter 6). Some lake deposits comprise an interesting exception, because sedimentary cycles can be related to absolute time, through cycles such as Milankovitch cycles. Early Triassic lake deposits of the Newark Basin demonstrate rapid speciation and multiple evolutionary radiations in semionotid fishes; six species appeared in the first 5,000 to 8,000 years of the recorded history of the lake (McCune 1996). This rate compares favorably with data derived from cichlid fishes in an African rift valley lake. The exact details of speciation cannot be followed in the fossil lake, but the dynamics of change of species diversity can be followed well.

If we can't easily study speciation in action, we should at least be able to describe why any two species differ and what is the reason that two populations are reproductively incompatible. Even if there is an obvious primary explanation of current incompatibility, one cannot be sure that this was the original incompatibility that caused speciation. Indeed, the theory of reproductive character displacement (Brown and Wilson 1954) argues that premating isolation mechanisms result from selection against hybridization, owing to the presence of ecological overlap. Premating isolation might also evolve in allopatry, as a by-product of some other selective force on life cycles (Krebs and Markow 1989). The complex history of speciation may therefore include divergence, evolution of sterility barriers between separated populations, and further evolution of premating barriers established during sympatry. This is likely the dominant story behind species origins.

Macroevolution as I defined it in chapter 1 seeks explanations of diversity on large taxonomic scales. Many have focused on the species level as a fundamental generator of diversity, arguing that speciation is a paroxysmal event, of a different kind from normal intrapopulation processes. Can interspecific differences in phenotypic traits be extrapolated from intraspecific differences? It is useful to distinguish between *polymorphism,* in which genetic variants are freely intermixed within a population, and *polytypism,* in which certain variants are fixed in distinct populations that have some probability of either diverging further into species or merging again, maintaining the existence of a single species. It is the extrapolation from polymorphism, to polytypism, to distinct species, that would constitute an intra–interspecific extrapolation hypothesis (Figure 3.2). If this hypothesis failed, one might have to invoke special species-forming mechanisms.

Intraspecific Variation

Natural selection and intraspecific phenotypic variation. *Natural selection* is a process that follows from the necessary conditions of (a) genetically based phenotypic variation and (b) differences in reproduction or survival among the variants. With these two necessary conditions, it follows that (1) if the population is out of equilibrium, then the phenotypic distribution of the offspring in a population will differ from that of the parents, or (2) the phenotypic distribution will differ among age classes, beyond that expected from normal ontogenetic change (see Burian 1983; Endler 1986). The logical consequences – 1 and 2 – following conditions a and b constitute a syllogism, not a tautology (Endler 1986). The misconception of a tautology stems from the phrase "survival of the fittest," which ignores the logical structure of conditions and consequences. Natural selection can also be applied to

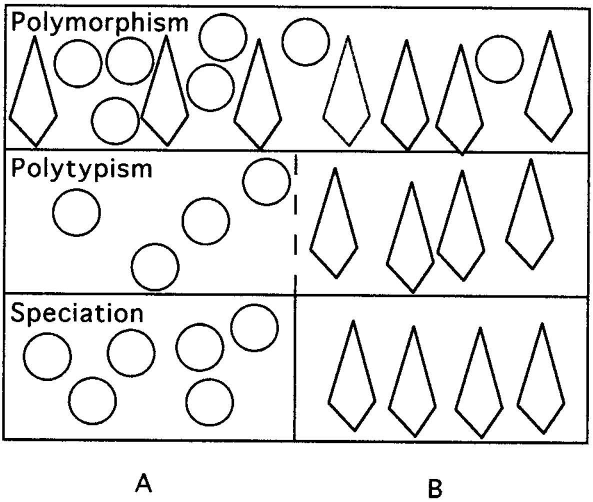


Figure 3.2. The transition between polymorphism (with clinal variation from A to B), polytypism, and speciation.

higher levels of the organismal hierarchy (see chapter 1). At the species level, for example, species with their traits constitute the variation, and the analogous measures of reproduction and mortality would be speciation and extinction. The consequence would be changes in the abundance of species. Each hierarchical level must have its own distinct heritable variation and a measure of productivity that could differ among the units. As long as the levels are decomposable in the hierarchical sense, the process of natural selection and even adaptation could be applied to levels above those of the individual.

If the change in phenotypic distribution is consonant with predictions based on a criterion of performance (e.g., owing to natural selection, tolerance to low salinity increases when salinity greatly decreases), then *adaptation* occurs. Adaptation is the historical process of evolutionary change describing how natural selection interacts with functional and developmental constraints, mutational availability, and random processes. Natural selection is the specific part of adaptation concerned with available variation and the selective environment. By contrast, *adaptedness* is a static description of the functional superiority of one or another phenotype in a specific environment.

Models of natural selection and adaptation often make the assumption that there are two necessary elements to predict the course of evolution: (1) a predictable description of the relationship between genotype and phenotype and (2) a description of the environment that discriminates among phenotypes. There are good reasons to believe that this is too simplistic. First, genotype–environment interactions are such that one cannot catalogue phenotypes just by knowing the genotype. The environment must often be specified (e.g., Gupta and Lewontin 1983). Our definition of natural selection does not require a separation of adaptedness from historical circumstances, as we require a specification of genotype–environment interaction. To the degree that genotype–environment interactions and environments vary, the outcome of evolution is increasingly complicated.

The course of adaptation may be eccentric, depending on the genetic track taken during evolutionary change. It is well known, for example, that forward and backward selective change of the same morphological trait does not occur at the same rate, despite the imposition of similar selection differentials. Different genes may take a phenotype in the same overall direction, but evolution must work with the complex variability at hand. Differences in environmental history may also result in different adaptive tracks. The problem of history can be seen in a study of mutant strains of *Escherichia coli* that produce the toxin colicin (Chao and Levin 1981). In a well-mixed ‘aquatic culture, the colicinogenic strains are at an advantage only when fairly common. When sensitive bacteria are killed, their death causes release of nutrients at random to both types of bacteria. Colicinogenic strains have lower division rates and therefore lose out unless they overwhelm the system with toxin. By contrast, in agar, colicinogenic strains come to dominate even when initially rare. The latter structured habitat permits the colicinogenic bacteria to create a barren zone, which is rich in nutrients. They then can spread at their “leisure.” The fate of the gene is therefore locked up in its historical background.

We cannot overstress the distinction of natural selective forces from the genetic variation present at the time of an evolutionary change. Some have argued that evolution is contingent, mentioning the co-opting of peculiar structures to perform functions (e.g., the panda's thumb used for a sort of grasping). But this argument obscures the presence of a similar selective force that operates on many species with disparate morphologies and genes. A study by Huey, Gilchrist, Carlson, Berrigan, and Serra (2000) proved this point well. *Drosophila subobscura* was introduced to North America from Europe, where one could find a stable cline of increasing wing length with increasing latitude. After a mere two decades, a strikingly similar cline had developed in North America, which attests to the predictable power of natural selection. But the exact response of North American populations differed in that different parts of the wing contributed to the size changes, relative to the European populations. Apparently, selection was for overall wing length, but this was achieved with different sources of variability in Europe and America. It would be interesting if the traits that change in the two respective regions correspond to increased heritability of the different specific traits that responded to selection.

Through habitat choice, behavior decisions, and so on, organisms can alter their own environment. This means that to study natural selection properly, we must be able to describe the interaction between organism and environment that determines the actual selective regime (Lewontin 1983b). This often means that history could thwart the prediction of clear evolutionary trajectories.

Fitness is often used interchangeably with *adaptedness*. *Fitness* should refer to the relative ability of genotypes to survive and leave offspring. One can also define *fitness* in terms of alleles at a locus. If we have a locus segregating for two alleles, A_1 and A_2, let the respective fitnesses be W_1 and W_2. We can then define a *selection coefficient, s,* which equals $W_1/W_2 - 1$. If p is the frequency of A_1 and q is the frequency of A_2, then the change in p over one generation will be

$$\Delta p = \frac{spq}{\bar{w}}$$

where $\bar{w}$ is the mean fitness of the entire population. Changes in allele frequencies are therefore associated with a fitness parameter. This expression is oversimplified and applies to haploid organisms. For a more complete discussion of selection in diploid organisms, see Ewens (1969).

The assessment of relative fitness of genotypes at a locus implies a complete randomization of the background genotype (Lewontin 1974). In practice, this is nearly impossible to achieve, given the great difficulty of randomizing the background loci that are tightly linked to the locus in question. This problem is not trivial and is a major source of difficulty in interpreting the meaning of selection experiments. In a crude experiment, selection for variants at an allozyme locus may appear to be intense, simply because the locus marks part of a – or an entire – chromosome (contrast Powell 1971 with Yamazaki et al. 1983). A detailed study of fruit flies, using flanking markers at close map distance, designed to randomize the genetic background, typically requires the counting of tens of thousands of flies (Eanes 1984; Eanes, Bingham, Hey, and Doule 1985). Such studies, rarely done, show that fitness among protein phenotypes is probably much less than usually estimated, when linked loci are factored out (Eanes 1987).

It is difficult to measure with statistical confidence selection among genotypes differing in fitness by as much as 1%. Natural selection involving such levels and less, however, can exert significant evolutionary effects. To demonstrate that recessive lethal chromosomal mutants of *Drosophila melanogaster* lowered the fitness of heterozygotes by about 1%, Mukai and Yamaguchi (1974) had to score about one million flies. Such Herculean projects have been completed only rarely. One should remember that biologically significant selection need only be $s > {}^1\!/_2N$, and N is often 10^6.

We shall be mainly concerned with morphological characters whose determination has both a genetic and an environmental contribution. Let us assume further that variation in the phenotype can be arrayed as variation along a single axis of variation. This could apply to both continuously measurable and countable characters. Assume that the population variation follows a normal distribution, with mean = 0 and standard deviation = σ. Assume also, following the methods of quantitative genetics (see Falconer 1981), that the phenotypic scale is determined partially by an underlying genotypic scale. We can plot along the genotypic scale a fitness function, which depicts the relative success of different genotypes.

Total phenotypic variance can be partitioned into a variety of genetic and environmental components. For our purposes, assume that all of the loci determining a phenotypic trait are independent, there is no dominance, and that there are no genotype–environment interactions. We can then simply define *narrow-sense heritability,* h^2, as the proportion of the total phenotypic variance, $\sigma^2{}_\mathrm{a}$, explainable by between-allele effects, or the additive genetic variance, G_a. Define a selection differential, S_a, which represents the difference in the means of the selected and unselected adults. If our phenotypic scale variable is Z_a, the change will be

$$\Delta Z_a = (G_a/\sigma^2{}_\mathrm{a})\ S_a = h^2\mathrm{S}_\mathrm{a}$$

This formulation provides a convenient way of visualizing how selection on a continuous phenotypic character can be related to an underlying genotypic distribution.

The greatest problem with morphological or other complex traits is their probable association with a large number of loci located over widely spread parts of the genome. *Quantitative Trait Locus (QTL) Mapping* has been developed to establish linkage maps between morphological traits and molecular markers (see Lander and Schork 1994; Lynch and Walsh 1997). It is an extension of traditional linkage mapping of traits, only expanded to larger scales owing to the use of molecular markers, which are practicable when they are highly polymorphic, such as RFLP loci. If a QTL can be mapped to a relatively small chromosomal region, molecular methods might be used to identify specific genes involved in affecting the trait. This approach promises to shed tremendous light on the structure of many morphological structures and their genetic architecture. For example, Zeng, Liu, Stam, Kao, Mercer, and Laurie (2000) found 19 different QTLs underlying trait variation of the posterior lobe of the male genital arch between two species of *Drosophila.* The differences suggested strong directional selection acting on the trait in each species.

Modes of natural selection. In *directional selection* (Figure 3.3), the maximum value of the fitness function is shifted away from the mean (we use the right side as a convention). The success of a given phenotype might increase continuously with higher phenotypic value. But directional selection can involve *truncation selection* of the entire phenotypic distribution past an absolute or relative (e.g., upper 10% of the population) threshold. This might occur when allometric considerations prohibit animals larger than a certain body size to satisfy their maintenance energy requirements, or when animals larger than a threshold size might escape the grasp of a predator.

Complete and careful observations of directional selection in natural populations, where the adaptive significance is clear, are few in number (see Boag and Grant 1981; Endler 1986; Ford 1975; Seeley 1986). This should be no surprise, as selection intensities have to be quite high to show any dramatic change, and such selection will be temporary before a new equilibrium is achieved. A selection intensity among discrete morphs of only a few percent would be effectively invisible, given the swamping effect of collecting difficulties, statistical problems, spatially varying directional selection, and possible differing genotype–environment interactions in different subhabitats. Nevertheless, the outcome of natural selection has been appropriately inferred in a surprisingly large number of cases (see Endler 1986). Consider the following examples.

Over 100 species of insects in British industrial regions blackened by smoke are dark in color, relative to conspecifics in unpolluted areas (Ford 1975, chapter 14). In industrial areas, vegetation is often darkened with smokestack soot, and light-colored substrates, such as lichens, are killed off by pollution. In the moth *Biston betularia,* the black *carbonaria* variant is dominant over the recessive light-colored morph. Dark-colored morphs are preferentially killed by a variety of insectivorous birds when placed on trees with a normal lichen cover. The light mottled color blends with the background. Birds quickly locate the light morphs against the contrasting background of the blackened vegetation (Kettlewell 1955). Kettlewell's data suggest that the selection coefficient favoring the melanic gene must be about 0.5. This would easily account for the rapid spread of the *carbonaria* morph since the middle of the nineteenth century, from negligible starting frequencies.

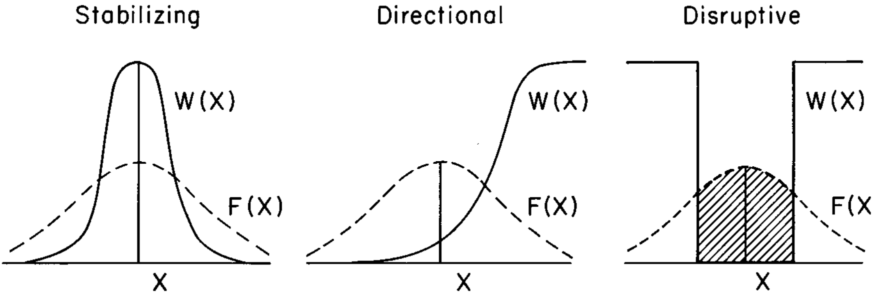


Figure 3.3. Examples of some modes of natural selection on a hypothetical normal distribution of phenotypes. Broken line is the frequency distribution of phenotypes; solid line represents fitness function.

Intense selection also has been observed in a population of one of Darwin's finches, *Geospiza fortis* (Boag and Grant 1981; Grant 1985). Parent–offspring regressions yield an average heritability of 0.76, for a wide range of external morphological characters. In 1977, the annual rainfall on Daphne Major island (Galápagos Islands) decreased drastically, which caused a dramatic decline of plants producing small seeds. The average size and hardness of seeds increased and larger birds fed more heavily on the large, hard mericarps of *Tribulus cistoides,* which had been ignored by almost all birds in earlier years. Large birds, especially those with large beaks, were able to survive because they were able to crack the large and hard seeds that predominated during the drought. The rainfall returned to normal the next year, suggesting that periods of intense selection probably occur at erratic intervals. Presumably, the selection for larger birds was reversed because of a return to normal conditions and size will shift downward. A lack of intense selection will slow the reverse selection process. Some more recent evidence shows the action of stabilizing selection.

Laboratory selection experiments usually attempt to change the average value of a phenotypic trait by biased culling of phenotypes. Although deviations of several standard deviations can be achieved rapidly, this type of experiment would not reflect rates in nature. Anderson (1973) measured samples of a mixed culture of *Drosophila pseudoobscura* that had been left in high- (25°) and low-temperature (16°) incubators for 12 years. After 1.5 years, no significant divergence in body size had occurred. But after 6 years, and until the end of the experiment (12 years), a significant body size differentiation had developed (about 7%). Body size varied inversely with temperature, and approximately 40% of the total phenotypic variance could be ascribed to genetic variation. This change is consistent with the commonly observed body size clines in latitudinally widespread species of *Drosophila.* Rapid evolution in body size, therefore, can be effected by the physiological effect of temperature alone. The evolution of wing size in *D. subobscura* is a case in point (Huey et al. 2000).

The power of directional selection should be greatest in large populations. Genetic variability is lost more slowly in large populations, and Fisher's fundamental theorem of natural selection demonstrates that the potency of natural selection is proportional to the genetic variance in a population. This is in contrast to the belief that small peripheral populations should be the site of most adaptive evolution. Experiments and theory demonstrate (Hill 1982) that large populations sustain more directional change than small ones. Thus, theory and observation refute the belief, popularized by supporters of punctuated equilibrium (e.g., Eldredge and Gould 1972) that small peripheral populations are of necessity the major source of adaptive change. Random (i.e., nonadaptive) forces operate most effectively in small populations.

Although large populations can sustain more directional selection, they may be spread over large areas with considerable environmental heterogeneity. If gene flow is sufficiently reduced, local populations may diverge, but a reestablishment of connection will dampen any directional shift. Large populations may therefore not accumulate much difference over long periods of time. If a broadly distributed species is divided into several geographically contiguous daughter species, then we might expect each of the daughters to go its own way. The daughter species would still have sufficiently large population size to sustain extensive directional change. Note, though, that speciation does not guarantee notable morphological divergence, as evidenced by the many cases of sibling species.

Stabilizing selection operates by culling out extremes from the phenotypic distribution (Figure 3.3). A modal phenotype is therefore favored. Stabilizing selection can occur in both continuous and discontinuous traits. In continuous traits, one would expect a range of variants, perhaps approximating a normal distribution on a linear phenotypic scale. Stabilizing selection for a modal birth weight is suggested by the survival of human infants, which is correlated with proximity to the mean birth weight of about seven pounds (Karn and Penrose 1951). In discontinuous traits such as number of segments, we must consider the model mentioned above for polygenic effects with thresholds, determining the discrete nature of the trait (e.g., *n* versus *n + 1* segments). Traits such as scutellar bristle number in *Drosophila melanogaster* are often strongly canalized, and extensive directional selection is necessary before the threshold is breached where variability is exposed (Rendel 1959). In less canalized traits of this sort, phenotypes differing from the mean number of (sternopleural) bristles show lowered fitness (Barnes 1968).

Stabilizing selection might be spotted in nature by sequential sampling of juvenile and adult populations. One might expect selective mortality to reduce the variance about the mean between juvenile and adult stages. Several studies have successfully recorded such a reduction, but the results are usually variable. Dunn (1942) recorded a reduction in variance of head scalation in the snake *Conopsis nasus* but got negative results for other species. In the gekkonid lizard *Aristelliger praesignis,* the variance of the number of toe lamellae decreases from juveniles to adults (Hecht 1952). Variance in two characters in a Cretaceous oyster diminished with increasing size (Sambol and Finks 1977). These results assume that between-generation differences in juveniles and adults correspond to within-cohort reduction of phenotypic variance.

Does any characteristic genetic structure underlie stabilizing selection? Directional selection should require a necessary reduction of genetic variance, assuming that the heterozygote does not determine the most extreme phenotype. Stabilizing selection has no such requisite. It might select for increasing heterozygosity if such genotypes determined intermediate values on the phenotypic scale. In an investigation of caudal fin ray number of the guppy *Poecilia reticulata,* in which stabilizing selection occurs, central phenotypes were found to be more heterozygous at allozyme loci than were extreme phenotypes (Beardmore and Shami 1979). Although the four loci examined were unlinked, older fish had genotypic frequencies that departed significantly from the multilocus Hardy–Weinberg expectation. This would suggest strong interlocus interactions on fitness. Much evidence demonstrates a correlation between genic heterozygosity and fitness, though the causal relationship is unclear (Mitton and Grant 1984).

Artificial stabilizing selection on sternopleural chaeta number (Thoday 1959) and on a wing vein trait (Scharloo 1964) in *Drosophila* both show a gradual decrease of phenotypic variance. This decrease includes a significant decrease of additive genetic variance, suggesting that the potential for evolutionary change (the response to selection) will decrease over time with stabilizing selection. These experiments, however, involve intense selection and may be unrepresentative of natural populations. If enough genes contribute to determine the additive genetic variance component of the phenotypic variance, then mutation may feed variation continuously into the population (Lande 1976).

In favoring those gametes with expressed phenotypic values close to the optimum, stabilizing selection may produce negative correlations in allelic effects at closely linked loci, so that positive and negative deviations from the optimum tend to cancel. This would create a pool of hidden genetic variation that is stored in linked combinations. Recombination would decrease the correlations among loci and convert the hidden genetic variation into expressed variation (Lande 1976). Thus, a mechanism for continuous generation of potential for phenotypic evolutionary change may be available. In the case without such negative correlations, where heterozygotes are intermediate in fitness, polymorphism will be lost from the population. Mutation feeds variability into the system and the polygenic nature of phenotypic determination increases the potential for mutation to increase the genetic variability affecting the trait. Stabilizing selection may therefore fail to reduce genetic variability sufficiently to keep a population from having a storehouse of variability capable of responding to directional selection. Schmalhausen (1949) argued that genetic variability is depleted during bouts of intense directional selection but is gradually restored during periods of stabilizing selection.

Selection has not eliminated variability. The omnipresence of considerable heritability for morphological traits suggests that selection cannot be a potent force for removing genetic variability from a population. As heritability is a measure directly related to the potential for morphological change, we can argue that most studied populations now seem capable of change as a response to selection. Unfortunately, our confidence about the universal variability seen in natural populations is not matched by a complete explanation of that variability (Barton and Turelli 1989, Houle 1989). There are complexities in the allocation of variability to allelic effects and remaining components explaining variation, such as environmental, epistatic, and dominance effects (Merila and Sheldon 1999). Nevertheless, there is widespread evidence of allelic variability of *morphological traits,* often thought to be under the control of weak stabilizing selection, and *fitness traits* (e.g., life history traits, sexually selected traits), which are assumed to be under the control of directional selection (Merila and Sheldon 1999). One might therefore expect that the latter traits should have less allelic variation but this does not appear to be so (Houle 1992). When standardized by the mean value of a trait, morphological traits actually have less absolute standing allelic variability than so-called fitness traits. It is true, however, that the environmental component of variance for fitness traits is greater, making their total heritability less than for morphological traits. The larger absolute allelic variation of fitness traits may relate to the larger number of genes throughout the genome that control fitness traits, relative to morphological traits (Houle 1992). While this may be true, sexually selected traits, including morphological traits, show much higher variability than naturally selected traits (Pomiankowski and Møller 1995), which is not very easy to explain except perhaps by strong local variations in sexual selection combined with gene flow.

Given the commonly high heritabilities, Kimura (1983, p. 143) made a rough calculation on the selection intensities at a locus, which I have modified slightly. Under stabilizing selection, the selection coefficient, *s*, equals

$$s = -[\log(1 - L_T)]h^2/n_{nuc}\mathrm{h_e}$$

where L_T is the segregation load, h^2 is the broad-sense heritability, n_{nuc} is the number of coding nucleotide sites, and h_e is the average heterozygosity. If we take 0.1 to be an appropriate value for detectable electrophoretic heterozygosity, and the hidden electrophoretic variability to increase this value by 100% (Selander and Whittam 1983), we would accept $h_e = 0.2$. Kimura (1983, p. 143) argued that we should use n_{nuc} as 3.5×10^9 to approximate the mammalian genome, but we shall use 3.5×10^8 to allow for a large percentage of non-coding DNA. Finally, we shall use 0.5 for the values of h^2 and L_T. With these assumptions, the selection coefficient is approximately 5×10^{-6}.

Such a low selection coefficient makes the probability of fixation close to the same order of magnitude as neutral evolution. The probability that a gene will be fixed by selection is

$$\mu = \frac{S}{2\,N\,(1 - e^{-s})}$$

where N is the population size, and $S = 4N_e s$. If we assume that population size is 10^9 and N_e is 10^6, our calculated selection coefficient of 5×10^{-6} yields a fixation probability of approximately 10^{-8}. If $N = 1000$ and $N_e = 100$, the probability is still only 10^{-4}. These calculations suggest that genetic drift may be a major component of the change of gene frequencies of loci in control of a trait. It must be emphasized, however, that such calculations are only averages; strong selection may be operating at many loci. This calculation makes the unrealistic assumption that selection would be spread equally over all loci. Any history of strong directional selection will bias downward the degree of accumulation of genetic variability at a locus. The degree of organization of the genome may also affect such an overall calculation. There is little evidence for widespread organization, but the presence of *cis*-acting enhancers, promoters, and functional multigene families complicates the picture. Finally, the pleiotropic effects (effects on several traits) of genes may reduce the opportunity for fixing mutations at a locus in the population. Selection for an allele affecting one trait may be inhibited if the incorporation of the allele would cause the fixation of another deleterious trait.

Let us now consider a morphological trait. The genetic variance generated per generation for a wide variety of organisms is approximately 10^{-3} times the total environmentally controlled variance for the trait (Lande 1980a). For single characters, the genetic variance generated per generation is approximately 10^{-3} per gamete per generation per character. A few thousand generations of random drift are sufficient to cause significant changes in the genetical component of the phenotypic variance (Lande 1980a). Lande argued that as the number of genes affecting a trait increases, the possibility for a continuous feeding of genetic variability affecting the trait increases similarly. Given the widespread observations of response to selection in various traits, natural populations would not be constrained to stay in the same place, except by stabilizing selection for intermediate phenotypes. Lande (1976) argued that a mutation–selection balance could maintain high levels of variability in natural populations in the face of strong stabilizing selection. Turelli (1984) argued that Lande's conclusions may depend on unsupported assumptions of the phenotypic effects of mutation, per-locus mutation rates, and the intensity of selection. Houle's (1998) compilation of mutation and standing genetic variance in *Drosophila* shows that mutational variance is highly correlated with genetic variance. Because most morphological traits can be changed rather easily by artificial selection, stasis, the long-term constancy of an average phenotypic trait in a population, must be due mainly to a lack of net directional selection, in combination with stabilizing selection and canalization, exhaustion of required genetic variability, or genetic correlations with traits whose change would cause a compensating loss of fitness. Canalized developmental programs, favored over the generations by stabilizing selection, might constrain future variation (see chapter 4). Aside from developmental constraints, long-term morphological stasis could involve two additional factors. First, a given morphology could be sufficiently restrictive that a loss or severe change of habitat would result in extinction. Therefore, a major part of survival of living fossils or in long-term stasis would be the survival of their habitat and a probable lack of superior competitors. For marine benthic animal species, the similarity of sediment habitat would likely maintain similarity of morphology. Stasis partially implies habitat restriction and habitat survival. Most habitat change is probably too extreme for the overall phenotype to survive. Stasis would therefore not be bound by any evolutionary constraint as much as it might be related to the blind alley created by habitat specialization.

The scenario here devised for stasis would involve a second crucial factor in evolution – the evolution of habitat selectivity. Of course, natural selection fashions the mechanisms of habitat choice, but habitat choice keeps the organism in the same milieu. What if the evolution of habitat specialization is suppressed? This causes selection for a generalized phenotype, capable of surviving a range of environments. The organism has some set of adaptations to respond to a wide range of challenges. By implication, this range of response is nongenetic in nature. Habitat choice permits the organism to choose its own selective regime. It is therefore incorrect to think of stabilizing selection simply as a culling process of phenotypes. As the degree of habitat selection changes, a continuous changing interaction develops between the selective effects of the environment and the organism's ability to choose where it will live. Thus, natural selection is not a disconnected process in which phenotype–genotype and environment are determined independently.

Disruptive selection favors phenotypes (Figure 3.3) at two or more modes in a potentially continuous distribution and acts against phenotypes in between the modes. This form of selection is important in a set of discrete environments, each favoring a discrete phenotype. In the short run, this form of selection is an efficient means of increasing allelic variance and is a mechanism for preserving polymorphism in a population. Disruptive selection can induce reproductive incompatibility and may be a mechanism for speciation (Thoday 1959). Combined with selection for host specificity, disruptive selection may be a mechanism for sympatric speciation (see Speciation Mechanisms).

Frequency-dependent selection occurs when the direction or intensity of selection varies with the frequencies of genotypes in the population. The rare-male effect in *Drosophila* (Ehrman 1967) is a case in point when rare male phenotypes are favored in mating, but this preference disappears as the phenotypes become more common. Frequency-dependent selection can generate complicated evolutionary trajectories when the animal is faced by conflicting selection pressures. Consider the selection imposed simultaneously by predation and mate choice. If a brightly colored male morph were present in low frequencies, it might be favored as a mate over its pale-colored competitors. It might also be conspicuous enough to be taken preferentially by a visually oriented predator. If predation were relaxed, the colored morph might increase in frequency. This would dampen selective predation, as all morphs would be similar in appearance. But colored morphs might lose their advantage as conspicuously rare potential mates (see Endler 1978).

Selection and geographic variation. Huxley (1939) coined the term *cline* to emphasize geographic variation in morphological and genetic traits as a common feature of natural populations. Clines may follow a linear pattern of differentiation with geographic space or may consist of two homogeneous populations that intergrade in a spatially restricted *step cline*. All genetically based clines must be explained as a combination of the processes of drift, gene flow, and selection. *Gene flow* is the process of successful movement of genes from one subpopulation to another and is a function of dispersal and viability success when the dispersing genotype reaches the target population. A cline may result from *primary intergradation*. Here, some spatially varying environmental property causes geographic variation in selection. Alternatively, *secondary contact* involves recent geographic mixture of two formerly differentiated populations. The cline might be maintained by mortality of both differentiated populations in the transitional zone. The processes of primary intergradation and secondary contact figure importantly in some models of speciation (see below).

Although clines are easy to document in either genetic or morphological terms, the shape or width of a cline varies in response to dispersal, genetic mechanisms of character determination, and selection intensities (Endler 1977; Slatkin 1973). For example, step clines may indicate a sharp ecotone or may simply be due to a smooth selection gradient with continuous but reduced dispersal. Step clines can be produced by selection pressures that are effectively unmeasurable in natural populations (Endler 1977). Increased dispersal distance will increase the width of a cline. Even in a cline, isolation may result in the presence of unique alleles at either end of the cline (Slatkin 1985).

Clinal variation in natural populations often suggests that gene flow is restricted, at least at the loci controlling the traits in question. For example, many studies have documented extensive latitudinal variation for physiological traits (Levinton and Monahan 1983; Lonsdale and Levinton 1985a, 1985b) and life history traits (e.g., Conover and Present 1990). Such differentiation may retard gene flow between geographically contiguous populations. Poor physiological performance of dispersers into adjacent populations may enforce sufficient isolation to permit gene flow restriction across the entire genome. This may permit differentiation to occur at other parts of the genome where selection pressures normally would be too small to counteract the effects of gene flow from adjacent populations. Such a process, termed *accelerating differentiation* (Christiansen and Simonsen 1978; Levinton and Lassen 1978), might be the cause of differentiation over much of the genome.

Some clines are shaped continually by natural selection. Williams, Koehn, and Mitton (1973) examined latitudinal differentiation in juveniles of the American eel, *Anguilla rostrata.* The species breeds in a restricted area of the Sargasso Sea and the newly born juveniles migrate to a series of localities along the east coast of North America. Nevertheless latitudinal clinal variation was found in juveniles indicating a period of selection at the allozyme loci examined or at linked loci. In the blue mussel *Mytilus edulis,* a steep cline into the estuarine Long Island Sound (New York) from open ocean habitats is probably under the control of active selection. Immigrations of juveniles marked by open ocean genotypes disappear with distance into the estuarine Sound, forming a steep cline. Selective mortality probably occurs with every larval settling season. Estuarine and open ocean populations show strong differences in tolerance to salinity stress (Levinton and Lassen 1978). Multilocus differentiation may greatly enhance the degree of gene flow restriction across a cline. Barton (1983) considered a simple model, in which weak selection against heterozygotes is assumed, presuming that alternative homozygous genotypes usually would be favored with selection in a gradient, if the location in the gradient were isolated from other populations. Introgression between adjacent populations depends on the selection intensity at each locus, the rate of recombination between adjacent loci, and the number of loci involved in the differentiation. As the degree of selection increases, relative to recombination, the barrier to gene flow is increased. If selection intensity and recombination rate are both kept constant, the barrier effect increases with the square root of the number of loci involved. The role of selection in retarding gene flow is strong if the number of loci involved is large.

Stochastic components of evolution. Random change in the genotypic constitution of populations – *genetic drift* – may be a strong component of genetic change. If we have a series of subdivided populations, such random forces might result in a series of populations, with alleles of a locus differing as the result of drift (see the discussion of Wright's shifting balance theory below). The time required to fix an allele by drift is roughly the order of the effective population size. Thus, drift cannot be a very important force in even moderate-size populations, unless there is no selection and no long-term gene flow from other populations.

The possibility of drift is an unsolved question of population genetics. To what degree does random evolution contribute toward adaptive evolution? The neutral theory of evolution asserts that sequence changes in protein evolution result from random gains and losses of alleles in populations (see Kimura 1983; Kimura and Ohta 1971). In a finite and isolated population, as genes are transmitted from one generation to the next, random sampling effects result in the loss and gain of frequency of variants (Figure 3.4). The same phenomenon holds for larger populations, though the probability of loss and fixation of alleles diminishes to a large degree. Random loss or fixation of an allele depends on population size, gene flow from adjacent populations, mutation, and selection. Founding populations are often small, which would also heighten the probability of random forces in determining the alleles that founders contain.

To determine the nature of sampling effects, we must measure the *effective population size* (N_e), which is an estimate of the number of individuals contributing gametes to the next generation and the relative contributions of gametic types by different sexes. Effective population size can be far smaller than absolute population size and is especially diminished when populations fluctuate widely. Under such conditions, the effects of random sampling error are largest during those times when population size is minimal. When populations fluctuate cyclically, effective population size is calculated as the harmonic mean of population size over the number of generations considered (Wright 1938). Strong bottlenecks diminish N_e still further (Motro and Thomson 1982). Variation in offspring number can diminish N_e. Effective population size also decreases with increasing skewness of the sex ratio, as the probability of random transfer of gametes diminishes because of the disproportionate contribution of genes to the next generation by the rarer sex. If a herd is dominated by one male, for example, its gametes reach the next generation disproportionately. The neutral theory of molecular evolution states that the rate of fixation of new alleles is mainly due to mutation and random fixation-loss processes (Kimura 1983). Although a large number of mutants may appear in populations, the majority will disappear by chance. This applies also to advantageous mutants, which can be lost when they first appear and are rare. The probability of fixation of an advantageous mutant with a 1% selective advantage is approximately 0.02 (Haldane 1927). Most neutral, mildly deleterious, and probably all deleterious mutants will not be fixed within a population.

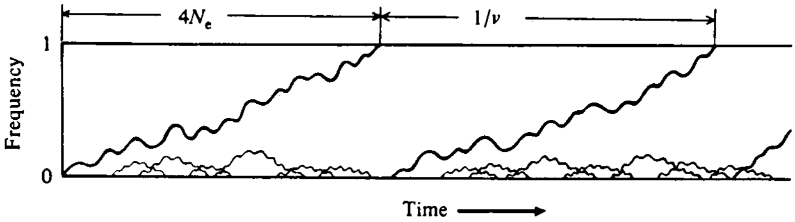


Figure 3.4. Behavior of mutant genes following their appearance in a finite population. N_e is the effective population size and υ is the mutation rate. (From Kimura 1983, with permission.)

The mutation rate at a given amino acid site is believed to be on the order of 10^{-6} per site per generation. Kimura assumes an infinite allele model: when a new mutant appears, it occurs at a new site in which mutant alleles are not already present in the population. Let υ be the mutation rate per gamete per generation. Given the presence of $2N$ chromosome sets, $2N\upsilon$ new mutants appear in each new generation. If μ is the probability of any one mutant's ultimately being fixed within the population, then we can calculate the rate of substitution, k, as

$$k = 2N\upsilon\mu$$

Given an assumption of an infinite number of new alleles that can be generated with mutation, and that the low probability of mutation precludes any significant back-mutation, we can estimate μ, which equals $1/(2N)$. The fixation rate is therefore

$$k = \upsilon$$

The time to fixation for a successful neutral mutant is $4N_e$. Assuming a model of random and possibly repeated mutation at a site, k for amino acids should equal $S_{aa}/2T$, where S_{aa} is the number of amino acid site differences between homologous proteins in two species and T is the time of divergence.

Although the overall fixation rate should be constant, the pattern of fixation on a small time scale will be erratic. Figure 3.4 shows that most mutants will be lost. A few will gain in frequency and will be fixed in the population. Because the fixation rate is predicted to be on the order of 10^9 per nucleotide site per generation, we would not expect to see a constant pattern unless we examined trends covering many millions of years.

The alternative *selectionist model* would predict the following rate of fixation, where s is the selection coefficient:

$$k = 4N_e s\upsilon$$

Effective population size is an important part of the fixation process. This would suggest divergent rates of evolution among taxa with characteristically different effective population sizes. This depends on the assumption that each new advantageous mutation is unique. Variation in selection would also suggest strong variability in rates of evolution among taxa and at different times within the history of a clade.

It is widely accepted that stochastic and selective factors contribute to the presence of polymorphism and to the fixation of alleles in natural populations. The contributory evidence can be summarized as follows:

1. Natural selection, often with high values of s, has been found widely in wild populations (e.g., Endler 1977; Mitton 1997).
2. Proteins with fewer apparent functional constraints evolve more rapidly than do proteins with many structural constraints (Kimura 1983).
3. Silent nucleotide sites nearly always evolve more rapidly than do sites that determine amino acid substitutions.

4. Pseudogenes and other noncoding sequences evolve at faster rates than do coding sequences.
5. In allozyme polymorphisms, common alleles are often abundant in sister species, and multiple clines are often found in widespread populations that show the same relationship between allele frequency and an environmental gradient (e.g., latitudinal clines on different continents and in the northern and southern hemispheres). This suggests selection, which preserves the allele frequencies despite isolation (Oakeshott et al. 1982, 1984).
6. For allozyme loci with multiple electrophoretic variants, even more are found within each electrophoretic class. This is usually not true for allozymes for which there are just one or two electrophoretic classes, suggesting a range of selective values in the two end-member types of allozyme polymorphisms (Eanes 1999).
7. Patterns of sequence variation suggest the importance of natural selection at many protein-encoding loci. Variation at silent sites are often conspicuously low in polymorphism. Selection sweeps away neutral variants of nucleotide sequences that are closely linked to sites that are selectively important (Kreitman and Akashi 1995).

Alas, this list suggests that polymorphism is rampant, but its causes are complex. But we are concerned with species and how variation within populations can be related to interspecies divergence. Perhaps it is sufficient to know that variation is retained.

The Link between Intraspecific and Interspecific Differentiation

The genetic transition in speciation

Gene trees and separation of populations into species. As two populations are separated, an important conflation may arise between population separation and inheritance of the two offspring populations of alleles from the ancestral population. Consider a genetic locus of an ancestral population that separates into two, with two prior coexisting alleles. Alleles of a locus may be inherited by both subpopulations, but one may be lost by genetic drift or selection. As a result, trees of gene divergence are not exactly the same as trees of population divergence (Figure 3.5). The complex pattern of survival and divergence of genes at first makes it quite difficult to discern patterns of monophyly of species from gene trees. It is possible that gene histories map concordantly to population subdivision, but they may just as easily be inherited in a complex fashion, with alleles from one monophyletic line being apportioned, or not, into two species (Figure 3.5). As time progresses, however, stochastic extinctions of some gene lineages and expansions of others will probably result in divergences between the separated populations, leading to a concordance between gene lineages and populations, or *reciprocal monophyly.* The gene lineage in each new species will be monophyletic (Figure 3.6).

The gene-tree framework explains some of the basis for believing that speciation may not necessarily be a major threshold of evolution. Avise, Deette, and Johns 1998 quantified the time scale for the process of establishment of reciprocal monophyly of Pliocene-derived splits and concluded that it took at least two million years to complete, for a broad range of vertebrates. As we discuss below, in many cases

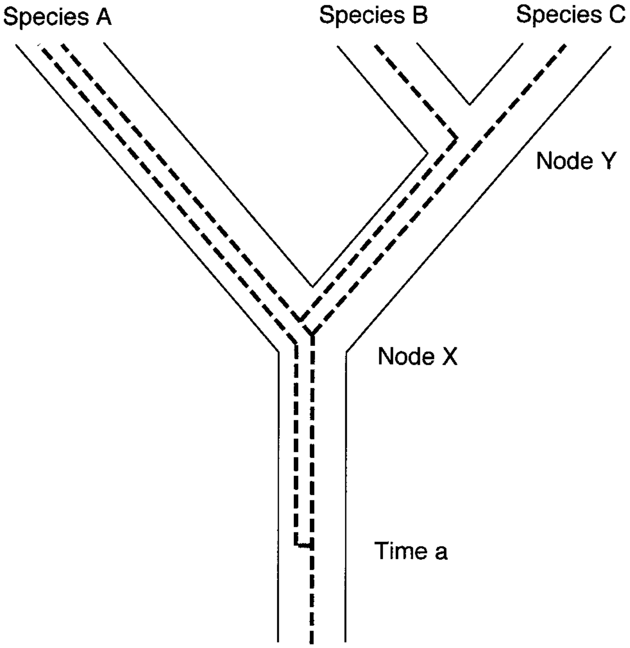


Figure 3.5. Relationships between gene histories and population divergence. Nodes refer to population splits, resulting in species formation. At time *a,* a gene lineage splits into two. At node *X,* both gene lineages survive in separated species A, but only one survives in the right-hand lineage. At the time of population splitting at node *X,* another gene lineage arises and survives to node *Y* and in species B but disappears in the population leading to species C.

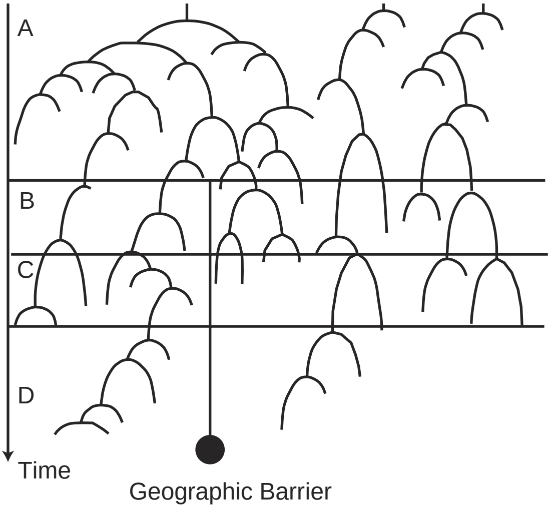


Figure 3.6. A complex history of allelic births and deaths is interrupted by a geographic separation at the end of period A. During periods B and C, the lineages in incipient species 2 are polyphyletic, but by period D, the complex ancestry is erased by extinctions and new alleles, producing monophyletic lineages of genes for each new species. (After Avise and Ball 1990.)

not only are most genes, functions, and alleles shared between sister species, but also there are many cases in which there is virtually no morphological difference that accompanies speciation. For example, the border between phenotypic plasticity within species often cannot be distinguished from interspecies differences among sister species (e.g., Knowlton, Mate, Guzman, Rowan, and Jara 1997). This suggests that the accumulation of genetic differences might be quite slow, even if the evolution of interpopulation sterility or ecologically significant differentiation might be much more rapid. It also suggests that the latter two processes are not necessarily coupled to this more gradual process and may be driven strictly by ecologically significant events.

Intraspecific and interspecific chromosomal variation

Modes of chromosomal differentiation. Chromosomal polymorphisms are generated by a large variety of chromosomal interactions. Rearrangements result from exchanges when two chromatids cross each other and exchange segments, or from breaks that develop while the chromosome is being stretched on the meiotic spindle. Breakage is usually followed by reunion with the same or another chromosome (White 1973, chapter 6). Rearrangements involve a variety of translocations, fusions, and reciprocal exchanges, which often cause strong reductions in gametic output. In the case in which a reciprocal translocation between two chromosomes results in one daughter with two centromeres and another lacking centromeres, the latter will be lost for lack of a spindle attachment. Chromosomal translocation polymorphisms can impose a high price on gamete viability. In the case of reciprocal translocation heterozygotes, gametes could have a duplication or a deficiency that, depending on the importance and interactions of the segment, may result in reduced viability or complete dysfunction of the gamete. In some dipterans, mechanisms exist for shunting aneuploid gametes into polar bodies. Paracentric inversions – resulting from two breaks on the same side of a centromere and inverting of the sequence – seem to have little effect on viability. Robertsonian fusions result when an acrocentric chromosome loses its short arm and fuses with another chromosome, usually another acrocentric. This seems to occur often with little negative effect, indicating that the short arms may contain mainly heterochromatin (noncoding repeated DNA).

Owing to the heterozygote disadvantage of chromosomal polymorphisms, we do not usually expect much chromosomal polymorphism; the spread of a new chromosomal variant will thus be difficult. Fixation of such a new variant will likely occur only in quite small populations by genetic drift (e.g., Lande 1979a; Wright 1940). This may not apply to some rearrangements, such as paracentric inversions in *Drosophila,* rearrangements in which crossing over is suppressed, situations in which aneuploid gametes are lost in polar bodies, and cases in which the effects on gametes are rather modest.

Even where the spread of a new variant is suppressed by heterozygote disadvantage, gene flow may occur between adjacent populations through combination with other chromosomes where no such heterozygote problem exists. As newly fixed rearrangements accrue in the genome, the possibility for complete incompatibility with other populations may increase. In *Mus,* the effects of multiple chromosomal heterozygotes are cumulative. Thus, a species with a transient polymorphism might differentiate into a series of chromosomally distinct populations (i.e., a polytypic species). As each separated population differentiates further, a series of new species might arise.

The chromosomal inversion polymorphisms of *Drosophila pseudoobscura* were described in great detail in the famous *Genetics of Natural Populations* series, written by Theodosius Dobzhansky and his colleagues. Most populations are polymorphic for paracentric inversions on the third chromosome, and geographic variation, ascribable to selection, is common (Figure 3.7). Although the mechanism of speciation is unknown in this group, inversions seemed to be passed on to new species. *D. persimilis,* for example, shares the *Standard* inversion with *D. pseudoobscura* (Olvera et al. 1979). The *Treeline* inversion is widespread throughout the range of *D. pseudoobscura* and may have given rise to other variants. Genealogies can be established using inversions, in much the same way that other characters can be used (e.g., White 1973, chapter 11).

Inversion polymorphisms of *D. pseudoobscura* vary in frequency spatially and temporally as the result of natural selection. Although spatial variations in inversions were originally thought to vary only according to stochastic processes (Dobzhansky

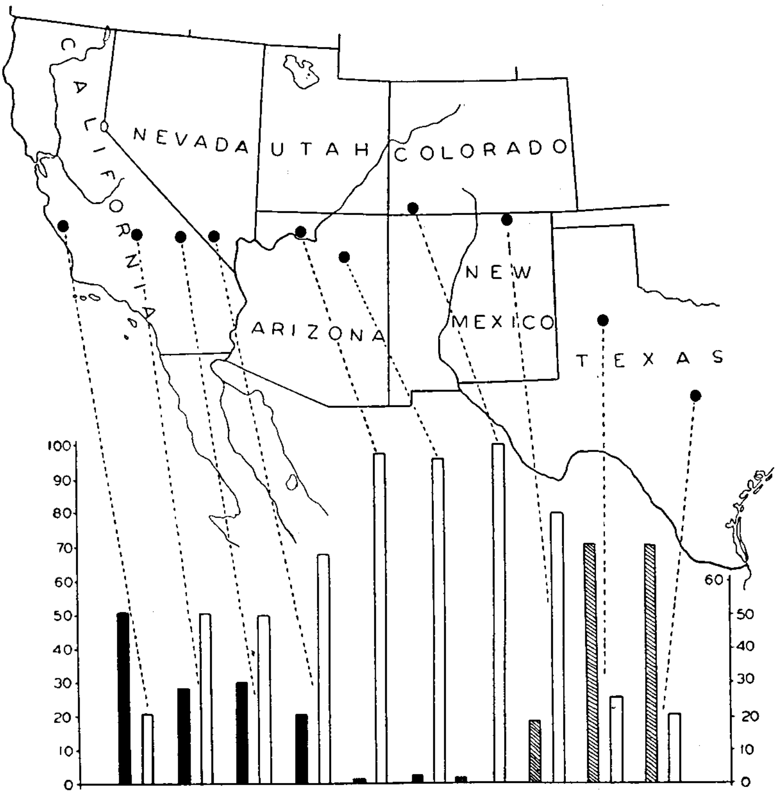


Figure 3.7. Frequencies of Standard (black), Arrowhead (white), and Pikes Peak chromosomes in populations of *Drosophila pseudoobscura* in the western United States. (From Dobzhansky 1947, with permission.)

and Wright 1941), later studies demonstrated correlations with altitude, season, and climate (Dobzhansky 1943, 1947, 1948a, 1948b). Some viability differences among individual organisms bearing different inversions may relate to the effects of temperature and crowding (Birch 1955). In some cases, strong regional differences in seasonal variation are related to climatic differences (Crumpacker and Williams 1974). In the cactus-loving species, *D. pachea,* a latitudinal cline of inversion frequency is strongly correlated with climate and a change of host plant (Ward, Starmer, Russell, Heed 1974). No evidence proves conclusively that these differences result from characters of the chromosomes per se, as opposed to alleles for specific genes or groups of genes, carried by coincidence.

Dobzhansky (1947) argued that chromosomal polymorphisms were the result of heterozygote (heterokaryotype) superiority. This was based on excesses of heterozygotes relative to Hardy–Weinberg expectations and the convergence to intermediate frequencies of two-inversion populations in laboratory cages. Frequency-dependent selection may also explain this convergence. Studies of overall performance tend to show that heterozygotes are superior, or at least equal in performance, to homozygotes. For example, Moos (1955) showed that homozygotes for the *Chiricahua* (CH) inversion were inferior in general physiological performance to *Standard* (ST) homozygotes, which were subequal in performance with CH/ST heterozygotes.

Heterozygote superiority seems to occur only when the inversions come from the same locality (Dobzhansky 1948b). This may indicate that superiority is conferred by favored gene combinations and not by any innate superiority of chromosomal heterozygosity.

Cases of chromosomal polytypism are found in a wide variety of species with limited dispersal ability and usually small population size, such as in small (particularly subterranean) mammals, some Diptera, and in flightless grasshoppers (Bush 1975; Key 1974; Nevo 1982; White 1973). Hybrid zones between chromosomal races, when present, are usually extremely narrow (e.g., Key 1974; Nevo 1982). This may testify to reduced gene flow between adjacent populations due to poor viability of chromosomal heterozygotes.

The distinction between subspecies and species status is quite difficult in situations of chromosomal polytypism. In the Central American Peter's tent-making bat, *Uroderma bilobatum,* two cytotypically characterized populations overlap in a small embayment in Honduras (Baker 1981). The two cytotypes differ by one terminal translocation and two fusions (2N = 44, 38). Gene flow is restricted, although the hybrid zone is claimed to be quite wide. Backcross cytotypes between the two populations occur over a band of 400 kilometers. Nevertheless, of 11 known polymorphic allozyme loci, 9 have markers unique to each of the populations (Greenbaum 1981). This suggests very restricted gene flow between the two populations, despite the claimed widespread "leakage" of chromosomes across the barrier. Barton (1982) suggested that the pattern of variation seen in the differentiation zone is consistent with a hybrid zone being maintained by hybrid unfitness. The apparent great width of the zone can be explained by the obviously large dispersal distance of bats.

Chromosomally distinct races (species?) are especially common in the house mouse, *Mus musculus.* The differentiation probably occurred in the past few thousand years and was strongly influenced by migrations of *M. musculus* with its commensal humans. But high speciation rates are also associated with many other small rodents, including *Microtus* and *Peromyscus* (Martin 1993). The unifying feature must be small effective population size, enforced by low dispersal, which is associated with small body size. Hybrid zones are narrow and hybrids often show strongly reduced fertility or malformations. The typical *Mus* karyotype in most localities consists of 2N = 40 acrocentrics. An isolated population in eastern Switzerland, however, is fixed for 2N = 26, suggesting the fixation of 7 fusions. This sort of isolation is common in Europe (see Capanna 1982). Populations with various degrees of fixed Robertsonian fusions occur in the Rhaetian Alps, the Apennines, and in Sicily. Fixations of different chromosome numbers divide populations according to region. In the Rhaetian populations, four metacentrics characterize all subpopulations. Other fusion types are found in successively more restricted subpopulations, until a given unit population is characterized by unique metacentrics. This suggests a process of isolation of a primordial population, followed by further substructuring into unique groups. Chromosomally distinct regions occur as islands in a sea of all acrocentric mice.

Populations of the mole rat *Spalax ehrenbergi* in Israel are also strongly polytypic, or show recent speciation (Nevo and Shaw 1972). Robertsonian fusions result in four major cytotypes (2N = 52, 54, 58, 60), which come into contact along narrow (2.8- to 0.7-kilometer-wide) zones. Paleobotanical evidence suggests that migration and subsequent differentiation in Israel occurred between 250,000 and 10,000 years ago. The four cytotypes are distributed along a north–south aridity gradient and are morphologically similar except for an inverse relationship between body size and environmental temperature. The subterranean habits and small population size of the mole rat are very conducive to such differentiation. Although premating isolation mechanisms usually exist between the cytotypes, one case still shows only postmating isolation, which suggests that postmating incompatibility preceded the evolution of premating recognition mechanisms (Nevo 1982).

Fixation of chromosomal variants in populations. In a randomly mating deme, the rate of fixation of rearrangements with large heterozygous disadvantage is minuscule unless effective population size is very small (Lande 1979a). Given known rates of fixation of chromosomal variants and spontaneous rearrangement rates, Lande estimated that long-term effective deme sizes must be on the order of 30 to 800 individuals for a wide variety of mammals, lower vertebrates, and insects. This suggests the ubiquitous occurrence of genetic drift in animal populations. The spread of chromosomal variants has probably occurred usually by random local extinction and colonization. Therefore, most locally fixed variants disappear when their population disappears via random extinction. Owing to their relatively minimal effect on heterozygotes, inversions and Robertsonian fusions seem to predominate over reciprocal translocations.

Rapid speciation of mammals, which seems to have occurred over time spans of thousands of years, is inconsistent with the average fixation rate of new chromosomal rearrangements, which is maximally on the order of one per lineage per million years (Bush, Case, Wilson, and Patton 1977). It may be that most chromosomally differentiated populations are geographically restricted and thus have a high probability of extinction. The more extensive populations, such as the all-acrocentric "standard" populations of *Mus musculus,* may survive owing to their abundance. In the random case, the probability of spread of a given variant over the entire species should be 1/*N,* where *N* is the number of demes. This probability, multiplied by the probability of fixation of a variant within a deme, would give the probability of spread through the entire species. To take the house mouse as an example, we can imagine that the number of demes must be sufficiently high that the probability of survival of the all-acrocentric karyotype is assured. New populations with novel genotypes will, for the most part, go extinct.

Chromosomal incompatibility may not prove to be the primary mechanism of isolation. Genic mechanisms of postmating isolation may be important even in chromosomally polytypic populations. In the rampantly speciating Hawaiian drosophilids, many groups of species are chromosomally monomorphic. On the other hand, extensive regional differentiation in chromosomal variants can occur with minimal reproductive isolation, as in the pocket gopher *Thomomys bottae* (Patton 1972). The phenomenon of hybrid dysgenesis in *Drosophila* is now known to result from genic disruption by transposable elements. Crosses between different strains result in accelerated mutation rates and chromosomal disruptions (Kidwell, Kidwell, and Sved 1977). Although the phenomenon is unrecognized outside of *Drosophila,* otherwise unknown alleles may be found in hybrid zones in mammals (Hafner, Hafner, Patton, and Smith 1983) and in other groups (Sage and Selander 1979; Whitt, Childers, and Cho 1973; Woodruff and Gould 1980; Woodruff and Thompson 1980). This may also reflect intragenic recombination in hybrid zones that may generate novel alleles.

A strong case can be made for gene-based sterility as a mechanism of postzygotic incompatibility. In *Drosophila melanogaster,* fixation of new genes in a population has a considerable probability of ensuring reduction of viability of offspring produced from crosses with other populations. At the X chromosome, fixations at about 9% of the genes would result in major sterility problems in females (Gans, Audit, and Masson 1975). In considering genes that affect more subtle aspects of mating behavior and reproduction, the potential for incompatibility is greater. Male hybrid sterility is explained similarly by several to many genes, particularly at the X chromosome (Coyne 1984). It may be, however, that the autosomes harbor as large a proportion of sterility factors as the X chromosome (Hollocher and Wu 1996). Genetic difference per se does not, however, guarantee postmating incompatibility. Cases of extensive chromosomal differentiation are known where reproductive compatibility is high. In the goodeid fish *Ilyodon furcidens,* extensive variation in the number of metacentric chromosomes occurs within a single river basin, despite minimal allozyme divergence and full viability of laboratory crosses and backcrosses (Turner, Grudzien, Adkisson, and Worrell 1985).

The extrapolationist hypothesis is consistent with the chromosomal differences observed among species. The mechanisms of geographic differentiation are easily related to speciation mechanisms involving the establishment of postmating isolation. Variants can be traced across subsequently differentiated populations and species

(Olvera et al. 1979; White 1973). There is no intraspecific–interspecific dichotomy. It is not clear, however, that chromosomal incompatibility is a major genetic mechanism of speciation. Chromosome differentiation does, however, bear the signature of genetic drift.

Comparisons with morphological and allozyme divergence. Extensive chromosomal race formation can occur with little concomitant allozymic differentiation. In the peripheral relict pocket gopher species *Geomys tropicalis,* major changes in chromosome number are not accompanied by an unusual degree of allelic substitution (Selander, Kaufman, Baker, and Williams 1974). This seems to be common in cases of extensive chromosomal differentiation (e.g., Greenbaum 1981; Nevo 1982). An interesting exception can be found in Rocky Mountain populations of *Geomys,* where extensive among-population chromosomal differentiation is accompanied by strong allozymic differentiation (Penney and Zimmerman 1976). Such major differences within one genus suggest a degree of unpredictability of an allozyme–chromosome correlation, but the latter case argues for local drift.

The rate of chromosomal variant fixation is inversely proportional to body size (Bengtsson 1980). This may relate to the longer generation time or to greater vagility of larger mammals. With relatively infrequent reproduction and few young per brood, a chromosomal abnormality would cause a significant loss of offspring. In fecund animals, loss of a few young might be matched by increased health of survivors or accelerated production of a successive brood. Thus, change might be accommodated more easily in small-bodied species. Gene flow among larger and possibly geographically wide-ranging mammals is probably not an explanation for reduced divergence, because behavioral deme structuring is common among larger-bodied species (Bengtsson 1980). Although deme structuring does not guarantee reduced gene flow, it can permit such a restriction.

Relation to morphological evolution. Chromosomal polytypism can be correlated with geographically related reproductive isolation. The chromosomal differentiation itself probably represents random fixation in relatively small populations with low vagility. The accumulation of such fixations in isolated populations may contribute to reproductive isolation. Despite the widespread occurrence of chromosomal races, the evidence does not support any extensive concomitant morphological differentiation. For example, the three classic morphologically recognizable species of the mole rat genus *Spalax,* ranging from Russia to North Africa, represent at least 30 karyotypes, most of which seem to be distinct species (Nevo 1982). Although the chromosomally distinct eastern Switzerland population of *Mus musculus* was once recognized as a different species on traditional grounds as *M. poschiavanus* (see Capanna 1982 and references), numerous other isolated races are morphologically indistinguishable except by karyotype. Great karyotypic disparity among species with few morphological differences can be observed in some rodents, foxes, insectivores, horses, and gibbons (see cited literature in Marks 1983).

I should emphasize that morphological correlations *can* be found with karyotypic differences. As an example, body size in grasshoppers seems related to the presence or absence of given inversions (White et al. 1963). This could be due to the presence of a few contributing genes, however. Most rearrangements seem unrelated to morphological differentiation. In *Drosophila,* rearrangements found in natural populations do not show any relationship to characters of taxonomic significance (Spieth and Heed 1972).

Chromosomal evolution has been claimed to be a cause of morphological evolution (Bush et al. 1977; Wilson, Sarich, and Maxson 1974; Wilson, Carlson, and White 1977). Under this hypothesis, chromosomal variants are regarded as having gene regulatory and morphological significance. If speciation is a cause of, or a concomitant process with, chromosomal evolution, then we would expect a correlation among speciation rate, karyotypic diversity, and morphological evolution. Rate of chromosomal evolution is assumed to be related to a measure of karyotypic diversity among extant species. Following the method of Stanley (1979), Bush et al. estimated speciation rate by taking the number of extant species and the time of origin in the fossil record for the group and calculating a splitting rate assuming constant dichotomous splitting. There was a positive correlation between the rates of chromosomal evolution and of speciation in a study of extant species of various reptilian groups and orders of mammals. From the correlation, they inferred that karyotypic evolution is a source of morphological evolution.

Although this is possible, a casual inspection reveals inconsistencies. Horses have the highest speciation rate and corresponding rate of chromosomal evolution. But the living forms whose karyotypic differences are extensive constitute a rather morphologically homogeneous group of mammals. A consideration of the fossil record of closely related horses does not increase the morphological diversity very much. Although correlated changes in body size, relative length of limbs, and hypsodonty characterize the grazing equine genera, morphological similarity is very strong, to the degree that minor reinterpretations of features in fossils have caused the systematic position of various groups to change radically (Woodburne and MacFadden 1982).

In contrast, the morphologically diverse Cetacea are lowest among the mammals in karyotypic diversity and speciation rate. The Sei whale, *Balaenoptera borealis,* and the common dolphin, *Delphinus delphis,* have nearly identical karyotypes (2N = 44), yet they must have diverged 40 million to 50 million years ago (Årnason 1972). Although the fossil record is too sparse to make an estimate of speciation rate, the Pinnipedia are similarly chromosomally homogeneous (Årnason 1972). As Bengtsson (1980, p. 38) noted, "…a relationship between karyotype evolution and the evolution of regulatory genes is, at most, of highly indirect and weak nature." The correlation observed by Bush et al. probably relates to the expected population genetic processes at reduced population size that occur during the speciation process. Karyotypic divergence is thus probably an effect of speciation, or even an occasional cause of reproductive isolation. It is not likely to be a major cause of morphological evolution.

Correlations between morphological and karyotypic evolution may occur, but only coincident with the speciation process. As an example, cladistic analyses of chromosomal banding patterns from 48 species of cryptodiran turtles, combined with fossil-based methods for estimating rates of karyotypic change, demonstrate that karyotypic evolution was twice as fast in turtle groups arising in the Mesozoic as in more recent splits and involved different forms of rearrangements. The deceleration in rate of change is correlated with decelerated morphological change. Some chromosomes have remained unchanged for at least 200 million years (Bickham 1981). Although chromosomal changes might be involved in adaptive changes, it is likely that the initial rapid radiation of turtles was accompanied by divergent morphological evolution, which must have involved speciation among geographically separated populations. In other words, speciation could have been an effect of divergent adaptation; the tempo of karyotypic evolution would probably have tracked speciation. Chromosomal change, therefore, was likely not the cause but was more likely the effect of evolutionary radiation and speciation.

Cherry, Case, Kunkel, Wykles, and Wilson (1982) used a metric, *D,* to estimate proportional differences in homologous skeletal measurements and found no substantial differences among species within genera of frogs, lizards, and mammals. Generic longevity of mammals is substantially less than for the others, and this might suggest that speciation rate accelerates mammalian morphological evolution. Alternatively, phyletic morphological evolution might be greater for mammals. Using Van Valen's (1973a) compilation, we can calculate the ratio, *R,* of *D* within a genus to the number of species per genus. If one assumes that the average number of extant species in a genus is proportional to the number of speciation events required to generate the species richness, then the divergence–to–species richness ratio gives a rough estimate of the relative amount of change realized per speciation event. One gets the following: mammals: $R = 1.90$; lizards: $R = 1.08$; amphibia: $R = 0.76$. A given speciation event or anagenic change during a species' history in mammals may therefore entail more morphological change than in reptiles or amphibia. The relationship between the rates of morphological divergence and of speciation may therefore be coincidental, or morphological evolution might even accelerate speciation.

This would solve a paradox well known to evolutionary biologists: The greatest amount of divergent evolution of morphology occurs near the beginning of the fossil record of a group. But this cannot be a time of maximum absolute number of speciation events, if any sort of exponential model of species increase applies. Thus, it is not the sheer number of speciation events but a qualitative difference in rate of morphological change that increases the degree of divergence per speciation event more toward the beginning of the history of a radiation. Usually, this seems correlated with the prior elimination of a competing group by a mass extinction (see chapter 7). It is therefore doubtful from this perspective that speciation per se accelerates morphological evolution.

Allozymes and interspecies divergence. Allozyme polymorphisms are ubiquitous in natural populations, although different groups may have characteristically different levels of variability (Avise 1994). Allozyme polytypism is also common among many species (e.g., Christiansen and Frydenberg 1974; Koehn, Milkman, and Mitton 1976; Schopf and Gooch 1971), though geographic homogeneity in allele frequency is also common (Ayala, Powell, and Tracey 1972; Prakash et al. 1969). Although the strength of selection at any locus is difficult to calculate, it is clear that natural selection plays a major role in the maintenance of variability, by means of fitness differences depending upon metabolic efficiency (Eanes 1999). A large number of studies, mainly in *Drosophila* species, permit estimates of the degree of intraspecific and interspecific differentiation.

Nei's (1972) index of genetic distance is commonly used to estimate allelic divergence at allozyme loci. If I_x is the average sum of the squares of the allelic frequencies over all loci for species *x*, I_y is the corresponding sum for species *y*, and I_{xy} is the average over all loci of the sum of the cross products of allelic frequencies for a locus, then distance *D* is

$$D = -\ln I$$
$$\text{where } I = I_{xy}/(I_x \mathrm{I_y})^{1/2}$$

I_x and I_y measure the average probabilities of identity over all loci of two randomly chosen homologous genes from species *x* or *y*, whereas I_{xy} is a measure of the average probability of identity of two randomly chosen homologous genes from the two species.

The data on the *willistoni* group of *Drosophila* (Ayala, Tracey, Hedgecock, and Richmond 1974) suggest a smooth transitional increase in *D* from geographic populations to morphologically different species. This seems to hold generally for animals (Nei 1975): Average D = 0.00–0.06 between races, 0.00–0.20 between subspecies, 0.1–1.5 between sibling species, and 0.1–2.5 between nonsibling species. The species barrier does not seem to be a special level of rectangular divergence in genic identity. If these degrees of differentiation correspond to stages in speciation, divergence seems to continue smoothly after speciation has progressed from the sibling species stage to a later stage of morphological divergence.

The smooth transition within a group of *Drosophila* might suggest an overall correlation between speciation rate and allozyme divergence among related groups. A correlation of genetic distance with the number of speciation events is compatible with punctuated equilibrium, but so is the greater accumulation of phyletic evolution in species that are undergoing speciation. This is especially relevant to ecologically driven speciation, where adaptation to environments leads to separation and eventually establishment of crossing barriers between newly established daughter species. Thus, although correlations between speciation rate and genetic divergence have been established (Mindell, Sites, and Graur 1990), it is only *lack* of correlation that proves anything, and such a lack of correlation falsifies a prediction of punctuated equilibrium. For example, the North American minnow family Centrarchidae is depauperate in species, whereas rapid speciation has been the rule for the sunfish family Cyprinidae (Avise 1977; Avise and Ayala 1976). In a study of 24 gene loci, average $D = 0.63$ for centrarchids, whereas average $D = 0.65$ for the cyprinids. This suggests a lack of relationship between speciation rate and divergence rate. The neutral theory would predict similar divergence among species if timescales since divergence were similar. Douglas and Avise (1982) extended the work to morphology and demonstrated that divergence among species is about the same between the rapidly speciating minnows and the more slowly speciating sunfish. Smith (1981) criticized this work, as the fossil record suggests a higher speciation rate for centrarchids than previously believed. Mayden (1986) thoughtfully analyzed the conclusions of Avise and colleagues and, although not disagreeing with their conclusion, pointed out many systematic difficulties, among which is the probable lack of monophyly of the minnows employed in the analysis. Avise (1994, p. 269) replied that if the minnows do not constitute a monophyletic clade, then they should be even older than now thought and should be even more genetically and morphologically distant among species.

There is no necessary relationship between morphological divergence and allozymic divergence. It is true that a good correlation exists in many species of mammals and fishes (Avise 1976). But many exceptions suggest that this may be due to rather constant correlated rates of morphological and allozymic divergence with time, with no causal relationship between the two sets of traits. In the desert pupfish *Cyprinodon macularius,* significant among-river morphological differentiation is not accompanied by allozymic differentiation much greater than is usually found in intraspecific comparisons of other teleosts (B. J. Turner 1983). This suggests that morphological differentiation can be rapid and independent of an allozymic scale. A similar discordance exists between patterns of color and banding and allozymic differentiation in Pyrenees and Welsh populations of the land snail *Cepaea nemoralis* (Jones, Selander, and Schnell 1980).

Morphology. It is difficult to summarize adequately the evidence for intraspecific versus interspecific divergence in morphology. In the case of chromosomes and allozymes, one has at least the confident feeling that identifiable markers can be traced across intraspecific and interspecific barriers. In the case of morphology, different parts of the genome can exert significant control on a given trait. There is also no uniform criterion by which one can draw equivalence between any two external morphological traits. If intraspecific variation of color morphs in butterflies can be extrapolated to interspecific comparisons, what relationship does this have to wing shape or to time of pupation?

Consider a character that has two different states in two different species. Is there a leap in character state that can be explained only by a speciation event, or can intrapopulation polymorphism be used in a simple extrapolationist model to explain polytypism and interspecies differences? Two possible approaches can be taken. First, if hybrids and F2 generations can be obtained between the two species, quantitative genetics can be employed to learn whether the difference between alternative character states is saltatory and based on fixation of alternative alleles at one locus or whether it is polygenically controlled with extrapolation possible from within-population variation. (Remember that discrete morphs can also be polygenically controlled.) Even without a genetic approach, much can be learned from a comparative biometrical study of morphological variation at the intraspecific versus the interspecific level. But if intraspecific morphological variance is much smaller than interspecific morphological differences, one can always argue that strong directional selection occurs during the speciation event. On the other hand, if the levels of variance are about the same, one can argue that yet other characters are saltatory and one has not come across the "species-specific" characters.

Crosses between species and populations have been done extensively, particularly in plants in which interspecific developmental incompatibilities are smaller than in animals. The minimum number of genetic factors controlling the trait is estimated by comparing the phenotypic means and variances in the two parental populations and the F1 and F2 hybrids and backcrosses. Polygenic control and the consequent possibility of extrapolation are often demonstrated by the intermediate phenotypic scores in hybrids and the expansion of phenotypic variability in the F2. In cases in which intermediacy in the F1 is not found, threshold effects and polygenic inheritance usually turn out to be the rule (e.g., Green 1962; Wright 1934a, 1934b, 1935a, 1935b). In most cases, the minimum number of genes for morphological traits is typically estimated as 5 to 10, with occasional values up to 20 (Lande 1983). Ten independent genetic factors were estimated to be operative in an analysis of tomato strains where two varieties differed about 56-fold in mean weight. As the haploid number of chromosomes is 12, the actual number of factors is probably larger, with some chromosome-level linkage.

Though we cannot make any universal statements, some interesting cases of interspecific variation demonstrate that the extrapolationist hypothesis is supportable for most transspecific evolutionary changes. A remarkable case of extreme morphological differentiation has been discovered between two species of Hawaiian *Drosophila, D. heteroneura* and *D. sylvestris* (Templeton 1977; Val 1977). The pair are very similar by allozyme and cytogenetic standards but are strikingly different in head shape (Figure 3.8). A genetic analysis shows that at least six to eight independent genetic factors control the phenotypic difference. The effects of the factors are predominantly additive, on which is overlain a sexual dimorphism that is most likely connected by a sex-linked locus or loci whose expression is limited to males. The interspecific phenotypic difference may be quite important in premating isolation, but it could have easily evolved from intraspecific variability.

For the sibling species of *Drosophila,* genital morphology is the sine qua non of species-specific morphological characters. They often are the only means of diagnosis and likely constitute a principal mechanism of premating isolation. Differences between species are discrete; otherwise they would not be good species characters! Coyne (1983) analyzed genitalia differences among the siblings *D. melanogaster, D. simulans,* and *D. mauritania,* by substitution of different chromosomes in hybrids. Variation in genitalia is under the control of at least four to five genetic factors.

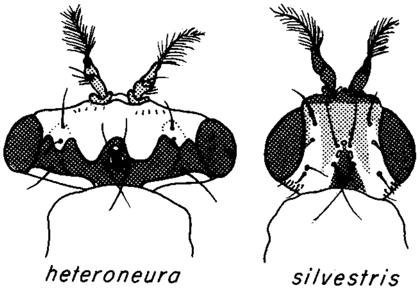


Figure 3.8. Discrete differences in head shape, despite polygenic trait control, between two closely related species of Hawaiian *Drosophila.* (After Val 1977.)

There is no need to invoke any unique process in the morphological differentiation accompanying speciation. A QTL mapping of the form of the posterior lobe of the male genital arch in *Drosophila simulans* and *D. mauritaina* shows the action of at least 19 loci (Zeng, Liu, Stam, Kao, Mercer and Laurie 2000).

Though species are morphologically distinct, one can find extensive regional differentiation, often equal in magnitude to interspecific differences. This can be shown, for example, in some species of the land snail genus *Cerion* on Caribbean islands (Gould 1969a; Woodruff and Gould 1980). Over distances of 100 meters, large changes in sculpture, size, and whorl number per unit size occur. Discrete, often major, variation is found commonly within species of marine snails, such as the genus *Thais* (Palmer 1985). In the three-spined stickleback *Gasterosteus aculeata,* intraspecific differentiation is pronounced and of the same order as interspecific differences (e.g., Bell 1976, 1981). Within a lake in British Columbia, two probable species coexist that reflect extensions of intraspecific differences (Larson 1976; McPhail 1984). The benthic form has a heavier body, wider mouth, reduced dorsal spines, and reduced lateral plates, relative to a limnetically specialized form. It is not clear that speciation occurred within this particular lake, but the body size, spine and plate polymorphisms are well known within other populations.

One example is of particular interest as it falls within the home territory of the macromutationist-speciation school. Mimicry in butterflies has been discussed above and shown to represent a polygenic system that evolved by accumulation of several new genes of varying relative effect on the phenotype. Can intraspecific variation be extrapolated to interspecific differences? Remember, this case was one of Goldschmidt's (1945a, 1945b) prime examples of the uniqueness of saltatory jumps.

Mimicry probably has the longest pedigree of any work integrating variation in natural populations with speciation. In 1862, Henry Walter Bates published a theory of mimetic resemblance among butterflies, stemming from his observations of intraspecific and interspecific variation in the color patterns of South American butterflies. Using the fabulous diversity of form found in Brazilian faunas, he was able to demonstrate a continuity between geographic varietal variation within a species and the common occurrence of small-ranging groups of species whose ranges were contiguous. To Bateson, this indicated that polytypism preceded speciation.

Turner (1981 and cited references) has investigated patterns of mimicry in the genus *Heliconius,* where Mullerian mimicry (model and mimic are poisonous) is the rule in both larvae and adults. The butterflies feed on passion flowers (Passifloraceae), which live in shaded forests. The genes involved in mimicry consist of a combination of genes of large and small effect. A large gene bridges a gap that permits the further evolution of stronger resemblance. Racial divergence within species is strong and is easily extrapolated to interspecific differences. The species pair *H. melpomene* and *H. erato* co-occur in a range of localities, each with its characteristic and quite different mutually mimetic color pattern. Laboratory crosses demonstrate complete interfertility among populations of the same species, taken from different locales. Nonmimetic relatives of both species have similar yellow and black patterns.

Brande (1979) investigated intraspecific versus interspecific variation within the genus *Mulinia* (Mactracea). *Mulinia lateralis,* for example, has a broad geographic extent from New Brunswick to Yucatán. It has given rise to one daughter species in Lake Pontchartrain, Louisiana – *M. pontchartrainensis* – and several related species also occur in the western hemisphere. Using discriminant function analysis, Brande found that the characters contributing to most of the among-locality variance within a species were also those important in among-species variation. This suggests that the features of the shell involved in intraspecific evolution are also those involved in the evolution of interspecies differences. Because shell characteristics are those expected to be crucial in bivalve adaptation (Stanley 1970), we can conclude that the speciation process is not particularly important here as a threshold in bivalve evolution. Similar results were obtained in an examination of the Miocene scallop *Chesapecten* (Kelley 1983a). Kelley (1983b) found that in some cases, characters most important in describing the variance within species were not those diagnosing differences between species. This proves little, because the "species" consisted of an ancestor–descendant series with no cladogenesis. How does one tell species apart, in this case, except by morphological change? Even in cases in which true species are examined, finding such a discordance between intraspecific and interspecific variance could also indicate that times of unique ecological change induce changes in characters of otherwise low variation. Unfortunately, Brande's test applies only to confirming the continuity of intraspecific to interspecific variation. A lack of continuity yields an ambiguous result.

Brande's results follow those of other studies. Clarke and Murray (1969) studied variation in *Partula,* a genus of terrestrial snails found in the Society Islands of the Pacific. Though it was formerly believed that many species occupied Tahiti and Mooréa, Clarke and Murray showed that only two species were present, with many individual races occupying a series of isolated valleys. Strong morphological differences may occur in direction of coiling, size, shape, and color – yet, many of the identified subspecies interbreed freely in the laboratory. There is good reason to believe that the differences among subspecies are due to genetic drift. In any event, the characters that may be used to distinguish among subspecies are the same that have been used to diagnose different species. In *P. suturalis,* those mitochondrial restriction fragment length polymorphism (RFLP) genotypes occurring within a population are usually separated by single-step changes. Mitochondrial genotypes can diagnose geographically coherent divergent populations. There is no detectable association between the mitochondrial genotypes and the occurrence of dextral or sinistral populations, showing that chirality does not constitute a genetic barrier (Murray, Stine, and Johnson 1991). The complete local fixation of either right- or left-handed chirality in subpopulations and species, however, may be influenced by difficulties in copulation between forms of different handedness, especially globose forms (Van Batenburg and Gittenberger 1996).

Brande's data on *Mulinia* allow a comparison of intraspecific versus interspecific variation. In general, the degree of intraspecific variation among populations was less than that among species. This might be explained by either (1) the power of the speciation process in morphological differentiation or (2) the passing of a sufficient amount of time to permit interspecific divergence to transpire via phyletic evolution. Apparently, the latter is the best explanation (Figure 3.9). The recently derived *M.*

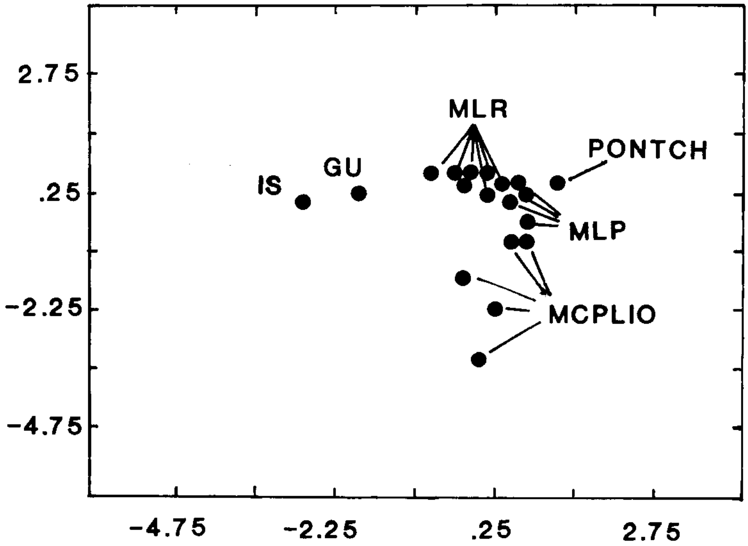


Figure 3.9. Discriminant function plot of first two axes for morphological variation within recent populations of the bivalve *Mulinia lateralis* (MLR), some Pleistocene populations (MLP), its ancestor the Pliocene *M. congesta* (MCPLIO), its descendant *M. pontchartrainensis* (PONTCH), and other recent species (IS and GU). (After Brande 1979.)

pontchartrainensis is barely on the morphological fringes of its progenitor, *M. lateralis*. The Pliocene *M. congesta* seems to evolve gradually into its descendant *M. lateralis*. In contrast, seemingly more distantly related species are morphologically more distant as well.

Stasis is used by proponents of the punctuated equilibrium model as evidence for a centripetal force in evolution. Stasis is said to imply a set of "...genetic and developmental coherences that resist selective pressures of the moment and impose a higher level, or macroevolutionary, constraint upon changes within local populations..." (Gould 1983b, p. 362).

This argument requires that (1) there be developmental and genetic sources of discontinuity and (2) that these sources be mobilized mainly at speciation. As we have discussed here and will in chapter 4, sources of discontinuity certainly exist. Our evidence, however, suggests that the sources are not associated with speciation. Yet species often are rather constant in morphology. Williams (1950), for example, found little intraspecific variation in cervical articulations in turtles. But some interesting, and quantum, variation could be detected in comparisons among species; is this due to the sort of "resistance" suggested by Gould?

Consider pharyngeal tooth morphology in fishes. Although strong interspecific differentiation is present, intraspecific variation in pharyngeal tooth morphology is relatively slight. This might argue for a centripetal force within the history of the species. A major ecological or genetic crisis might be required to cause the evolution of new forms. This hypothesis can be falsified by examining morphological variation in tooth morphology among clones of unisexual fishes of the genus *Poeciliopsis*.

Vrijenhoek (1978) found extensive differentiation among clones for trophically significant differences in dentary morphology, involving differences in number and arrangement of teeth (Figure 3.10). These differences coincide with interclonal niche differentiation in feeding behavior. Thus, when clones are formed, many specific and highly differentiated morphologies can be fixed within the geographic range of a species. Major variation typical of interspecific differentiation is thus present, ready to be tapped within any species population. This seems to be common among species of fishes (Vrijenhoek 1978). Stabilizing selection must prevent these combinations from usually appearing.

Therefore, a genetic revolution is not at all necessary to break a pattern of genetic homeostasis. Very likely, natural selection and gene flow prevent the fixation of radically new morphologies. Speciation might be correlated with morphological differentiation, but this is only coincidental with spatial variation in selection pressures. Of course, there are examples in which the introduction of a new allele can destabilize an otherwise regulated (canalized) trait, as in studies of the *scute* locus of *Drosophila melanogaster* and at the *tabby* locus in the mouse. But this does not have any necessary connection with speciation; it can occur as easily within a panmictic population.

Stanley's (1979) monograph on macroevolution, basically a plea for the importance of speciation in morphological evolution, unknowingly revealed the blurred distinction between his conception of speciation and divergent evolution, based on differing selection pressures in ecologically distinctive zones. He asked (p. 72): "Why should all populations of any established species abandon their original niche because adjacent ecological space is free for occupancy? Certainly, expansion of the original niche might be expected, but it is difficult to imagine that this could produce major adaptive shifts without fragmentation into new species. Far more likely would be the rapid invasion of adjacent ecological space in association with divergent speciation."

This association of speciation with occupancy of divergent habitats is precisely the same as a model of divergence based on differential selection of a polytypic

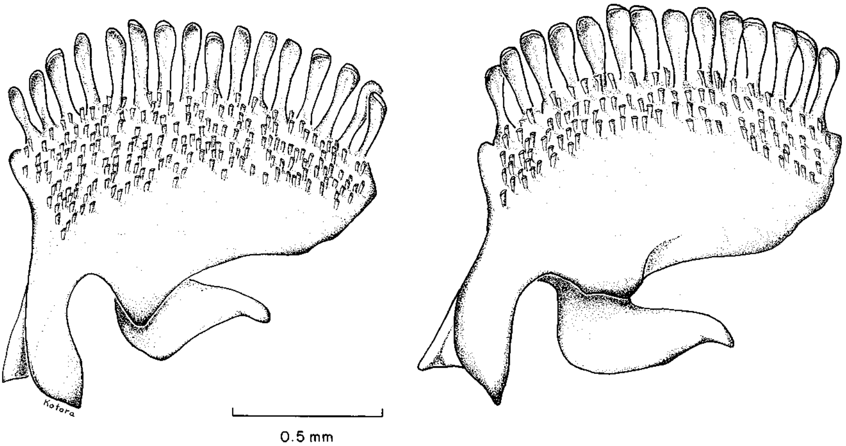


Figure 3.10. Two divergent dentary morphs, found in different clones of *Poeciliopsis.* These morphologies are associated with different algal grazing behaviors. (Courtesy of Robert Vrijenhoek.)

species. In other words, it is an ordinary neo-Darwinian model. The appearance of a new resource or habitat would exert strong directional selection, particularly if an old resource or habitat is less abundant.

In summary, patterns of geographic variation and genetic analyses of interpopulation and interspecific crosses and backcrosses fail to substantiate the idea that speciation is a special process with regard to morphological differentiation. Although one cannot say much for those characters that cannot be studied effectively, those amenable to genetic analysis only provide support for the intra-interspecific extrapolation hypothesis.

DNA-level molecular variation and interspecies divergence. Although allozyme divergence between species must correspond to molecular differences, the 1990s completely overturned our general approaches to species identification. Systematists and population biologists are rapidly turning to more direct molecular markers to track the differentiation of populations and species. Unfortunately, our disciplines are still at a formative stage and it is difficult to draw broad conclusions.

Molecular markers of divergence at the intra- and sister-species levels fall into the following classes:

1. *Restriction fragment length polymorphisms (RFLPs):* RFLPs are generated by incubating mtDNA with restriction endonucleases, which cleave DNA at specific recognition sequences four to six base pairs long (see Dowling, Moritz, Palmer, and Rieseberg 1996 for details). Complete digestion yields a set of fragments of different lengths, which can be visualized by means of electrophoresis. Extremely useful in population analysis, RFLPs also have been routinely used to identify isolated populations, presumably on the way to speciation. Indeed, they are one of a spectrum of tools that demonstrate the continuity between population differentiation and speciation, as opposed to there being a discontinuity (Avise 1994).
2. *Direct sequencing of DNA:* Protein coding genes, their introns, and other sequences provide an immense potential database for the characterization of populations and species. Sequences have the special value of data that are amenable to phylogenetic analysis, as they provide a set of alternative character states for specific sites, providing sequences can be matched among samples with confidence (see chapter 2). In recent years, new techniques and automation have made sequencing accessible to a wide community of population geneticists and systematists. Most data are restricted to a relatively low number of sequence types, owing to the problem of obtaining primers necessary for the PCR to work (Palumbi 1996). Aside from this and other methodological difficulties to overcome (see Hillis, Moritz, and Mable 1996), genes must be chosen that evolve fast enough to discern population differentiation.

   It is not my purpose to provide an exhaustive account of DNA sequence differences among species. As a by-product of the study of evolutionary relationships, many trees have been constructed among closely related groups of species. Some examples will be cited below. Species that appear to be sister taxa from morphological criteria usually turn out to be extremely similar in sequence, but admittedly most of our data are confined to a small number of genes, such as carbonic anhydrase I and 16S rDNA. My own experience with this comes from a study of the crustacean genus *Uca,* a pantropical genus of semiterrestrial crabs. The most recently derived species, *Uca panacea,* identified morphologically and by its characteristic mating wave (Salmon, Hyatt, McCarthy, and Costlow 1978), is nearly indistinguishable in 16S rDNA sequence from its likely progenitor, *U. pugilator* (Sturmbauer, Levinton, and Christy 1996). Given the restricted geographic range of *U. panacea,* it is likely derived from *U. pugilator.*

3. *Minisatellites:* These sequences come from hypervariable regions of repetitive DNA whose variants can be visualized by Southern blot technique and can be used to trace individuals in populations. Stringent methods are used to identify particular minisatellite loci. It is a population level technique useful for tracing paternity and familial relationships in structured populations (Avise 1994).
4. *DNA–DNA hybridization:* This method estimates the overall similarity of DNA of different taxa by the rate at which separated strands anneal. The argument is that more rapid annealing represents greater sequence similarity. Specifically, one "melts" DNA, separating duplex strands, and then follows the time course of annealing of DNA from different taxa, as compared with annealing of DNA strands from the same taxon. Then, reheating is done, which dissociates duplexes of different-sequenced strands with more ease than complementary sequences. The temperature at which 50% of the hybrid molecules remain in duplex condition is the usual data used in an analysis. One must assume that the number of nucleotide differences is proportional to the degree of sequence difference (repetitive DNA is removed). Unlike direct sequencing, this technique depends on similarity in hundreds of thousands of nucleotide sites but cannot properly estimate the exact sequence differences. It is therefore sort of a hybrid between genetics and something like a DNA set of calipers.

   DNA–DNA hybridization was used on a gargantuan scale by Sibley and Alquist (1983) to estimate species relationships among birds. Although there has been tremendous controversy in some of their conclusions, de facto, this method has sunk into history, owing to the ease of DNA sequencing.

Speciation Mechanisms

The models

Allopatric model: divergence and contact. The possible mechanisms of speciation revolve around two major issues: ecology and genetics. From the ecological standpoint, the geography of speciation has been a major point of disagreement. *Allopatric* models require geographic isolation between newly forming daughter species and sometimes predict strong genetic changes at the time of speciation. *Parapatric* models allow for some contiguity between diverging populations. *Sympatric* models assume the possibility of random contact and mating within a population; ultimately, a number of mechanisms separate the population into two or more new species. It is not often clear that these distinctions are appropriate; a continuum might be more accurate.

One major school of thought maintains that all speciation is associated with geographic separation (Figure 3.11). The *allopatric-dumbbell model* asserts that populations become separated by a geographic barrier. Populations on either side of the barrier are large and are genetically representative of the starting population, with the possible exception of some geographic variation. It is clear that dispersal and

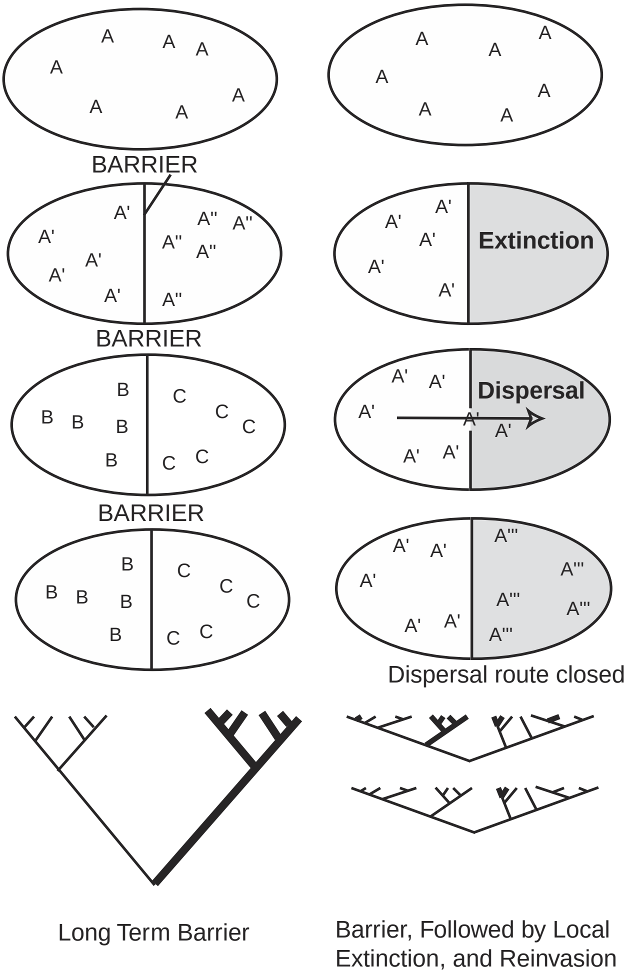


Figure 3.11. Two variants of the allopatric model. Left: A barrier divides a large population into two, and the cutoff of gene flow permits divergence, eventually to populations that do not reproduce, even if contact is reestablished. Right: After an extinction of part of a species range, a subsequent invasion into the area of extinction results in subsequent divergence.

gene flow, once disrupted, results in structured subpopulations, which eventually leads to strong differentiation (Bohonak 1999 and references therein). Subsequent divergent evolution on either side of a barrier may lead to accumulated genetic differences, related to the ecological differences between the isolated habitats (Dobzhansky 1937). Mating behavior, if it is unrelated to the ecological distinctness of the isolated regions, may not diverge, and individuals of the incipient species may mate freely.

Isolation: postmating and premating. The genetic differences acquired during isolation may, however, result in reduced viability of hybrids – *postmating incompatibility* – should the populations be reunited. We are largely ignorant of the mechanisms of such incompatibilities, except for *Drosophila.* After secondary contact between the diverging populations, postmating incompatibility between hybrids may result in selection against hybridization, resulting in one or more behavioral or morphological isolating mechanisms. From these, *premating isolation* may arise as the result of selection against hybrids. Premating isolation could also arise coincidentally when the populations are separated.

Mating behavioral incompatibility has been found in a number of cases of closely related *Drosophila* species. In *D. pseudoobscura* and *D. persimilis,* most effects on mating incompatibility have been mapped to a large number of locations on the X chromosome, with some interaction effects on the autosomes (Noor 1997). Females from a population of *D. melanogaster* geographically isolated in Zimbabwe typically reject individuals taken from other regions, when they have an alternative choice of a Zimbabwean male (Wu, Hollacher, and Begun 1995). Evolution of postmating isolation, registered on the X chromosome, appears minimal but is more likely focused on behavioral traits whose controlling genes are on the autosomes (Hollocher, Ting, and Pollack 1997). A physiological mechanism of between-species isolation may involve differences in female cuticular hydrocarbons (Coyne and Oyama 1995).

Postmating incompatibility presumably arises by random fixation of mutants that influence gamete compatibility, embryonic development, and so on. These would be expected to arise after populations become isolated from each other. Natural selection might also drag along alleles involved in incompatibility by means of hitchhiking. Most of our knowledge of genetic mechanisms of compatibility come from *Drosophila* species. Genes controlling traits vary from one to large numbers, and there is no a priori means of predicting which will influence compatibility. Genes implicated in postmating incompatibility are revealed by death of offspring of crosses or diminished viability of offspring. Many genes on the X chromosome affect survival of hybrids, although fewer genes seem involved in viability of offspring (Coyne et al. 1998). Sterility is often enhanced by the presence of specific combinations of genes, suggesting epistasis as a major force in the evolution of sterility (Cabot, Davis, and Johnson 1994). Sterility and viability are often severely reduced in heterogametic offspring of crosses between sister species (Haldane's rule). Unfortunately, there are inconsistencies in proposed explanations, such as interactions between the sex chromosomes and the autosomes (Coyne 1994). Haldane's rule is so widespread (Coyne and Orr 1989), even dominant in animal groups that one can't help but feel that the expression of genes either on or influenced by sex chromosomes is a key to understanding sterility.

One might argue that the development of sterility is really not speciation. If so, what is? We might argue that other traits might evolve in isolation, traits that have more ecological and physiological significance. But if the isolated populations reestablish contact, the degree of sterility resulting from interpopulation crosses may provide a strong selective payoff for avoiding hybridization. Coyne and Orr's (1989) compilation suggests that premating isolation is strongly enhanced in sister species of *Drosophila* that live sympatrically, when compared to allopatric pairs. Sympatric taxa show full isolation at Nei's $D = 0.2$, whereas a similar degree of isolation among allopatric species is not achieved until Nei's $D = 0.7$ (Figure 3.12).

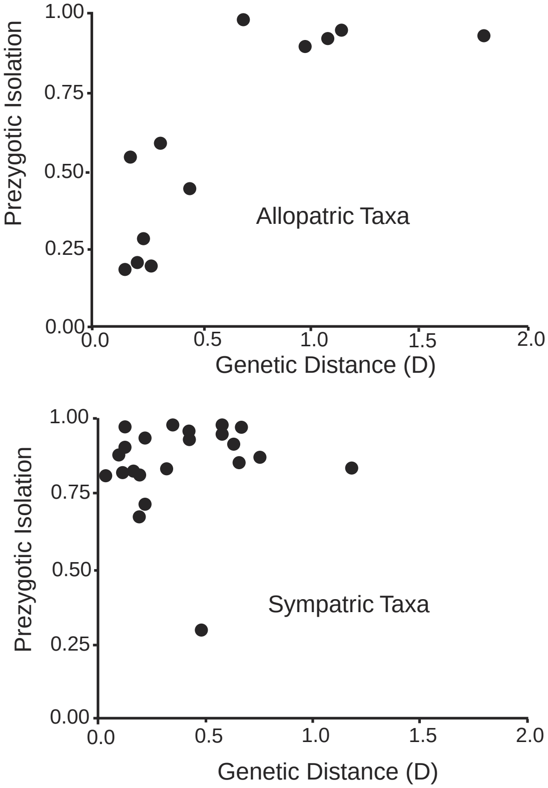


Figure 3.12. Strength of prezygotic isolation in allopatric and sympatric pairs of putative sister species of Drosophila. Allopatric species show much less prezygotic isolation over a broad range of genetic distances. (After Coyne and Orr 1989.)

Sexual selection and speciation. Sexual selection is a dynamic process and may continually propel populations in directions of new phenotypes, many of which are instrumental in mate recognition and competition. This alone can drive the process of isolation by premating differences, should the two populations come into contact. In fiddler crabs (genus *Uca,* family Ocypodidae), differences in claw-waving are probably associated with isolation (Salmon et al. 1978). An isolated population might therefore evolve rapidly and, as a side effect, it might be isolated in mating from its parent population. Arnqvist (1998) demonstrated that patterns of variation in genitalia are consistent with mating systems. By comparing sister clades, he found that genital evolution is more than twice as divergent in groups in which females mate several times than in groups in which females mate only once. No such difference was found in other morphological traits. These findings provide strong empirical evidence in favor of a sexual selection mechanism of the evolution of genitalia. In the renowned Zimbabwean population of *D. melanogaster,* mating isolation is genetically controlled on the autosomes and there is little postmating isolation from other populations. In this case, sexual selection has apparently been a driving force behind differentiation and perhaps speciation at the nascent stage without reinforcement.

We usually think of sexual selection as the force that changes color and form in animal males, leading perhaps accidentally to the divergence of separated populations. There is some compelling evidence, however, that sexual selection operates even at the time of fertilization. The *Odysseus* (*Ods*) hybrid male sterility locus of *Drosophila* contains a homeobox domain, which appears to have evolved rapidly in an estimated 500,000 years, even faster than an adjacent intron or protein-coding gene. Positive selection is the likely mechanism and may, as a consequence, promote divergence and the potential for the development of sterility. The *Ods* locus is known to function in male reproductive function, and sexual selection may be the driving force in rapid evolution.

A similar story is emerging for marine planktonic gamete recognition. Many coral reef species spawn at the same time, probably to maximize the probability of fertilization under certain hydrodynamic conditions (Clifton 1997, Gittings et al. 1992; Harrison et al. 1984). Thus, the gametes of many interspecies combinations may collide and yield inviable embryos unless some specificity of gamete recognition exists. In abalones, the sperm protein lysin forms a hole in the egg envelope, which is species-specific. Evolution of both lysin and the egg receptor protein is very rapid, suggesting a sort of escalational evolution. If two populations are separated, such rapid evolution could cause rapid divergence and loss of egg–sperm recognition between individual of different populations (Swanson and Vacquier 1998). Many studies have documented partial fertilization failure between distant populations and closely related species of sea urchins (Levitan, Sewell, Chia 1991), which may be related to similar processes involving the sperm protein bindin and its egg receptor. Bindin sequence polymorphism is common in urchin populations, but the egg receptor is apparently flexible enough to still allow fertilization (Metz and Palumbi 1996). The fixed differences between species may be central in the blockage of fertilization, but random differentiation in the polymorphic sequences might be the source of the rise of future isolating factors.

One might question the likelihood of marine isolation, but we have mentioned above the power of coastal barriers to isolate species and populations. Even over the expanse of the Pacific Ocean, isolation by distance has been detected in sea urchins (Palumbi, Grabowsky, Duda, Geyer and Tachino 1997), although the geographic scale is clearly much larger than might be expected in most terrestrial species.

Peripatric model. The *peripatric* model asserts that speciation occurs not by separation of large populations but by budding at the periphery of a species' range (Mayr 1963, 1982b). Gene flow and strong coadaptation within the genome are presumed to maintain geographic homogeneity in the main population. According to this hypothesis, small peripherally isolated populations are genetically unrepresentative of the parent population (founder effect). Mayr (1982b) noted that the "…gene pool of a small either founder or relict population is rapidly, and more or less drastically, reorganized, resulting in the quick acquisition of isolating mechanisms and usually in drastic morphological modifications and ecological shifts. It involves populations that pass through a bottleneck in population size." Intense selection combines with the founder effect to cause a "genetic revolution" resulting in a rapid genetic shift. Species divergence is thus accomplished. Alternating periods of population flushes and crashes may rapidly accelerate the breakup of coadapted gene complexes and cause divergence of sufficient magnitude to result in reproductive isolation from the parent (Carson 1975). The peripatric model is in the allopatric class, as it requires geographic isolation of the budded daughter population.

A common theme of speciation models (there are certainly others beyond the ones cited above) is the wedding of ecological to genetic mechanisms. The peripatric model, for example, requires a specific geographic configuration – budding peripheral to the range or in an isolated area within the range – and argues for a genetic revolution within the budded population. Mayr (1963) argued that a species' cohesion is maintained by gene flow, thus usually preventing divergence within the range of a species. It has been claimed that gene flow is not the mechanism of broad-scale homogeneity (Ehrlich and Raven 1969; Larson, Wake, and Yanev 1984). Uniform selection conditions throughout the range, accompanied by stabilizing selection, or even canalization of traits, probably combine to promote phenotypic homogeneity. Even if the genetic claims about peripatry may prove to be incorrect, peripheral populations do probably exist under ecologically divergent conditions. One must therefore make the distinction between the ecological context of speciation and the change in genetic architecture of populations during the speciation process (Templeton 1981).

Gene flow is one of the most difficult things to measure in natural populations. A direct approach requires measurements of dispersal and successful breeding of the successful immigrants. Moreover, these measurements must be done over timescales relevant to potential genetic change. Gene flow would prevent local differentiation, but the significance of gene flow depends on the strength of selection or drift. At a neutral polymorphic locus, an exchange of even one individual per generation on average would be sufficient to counter local differentiation by means of genetic drift. To counter natural selection, gene flow must be stronger as the strength of local selection increases. For gene flow to offset a fitness difference of 1%, 100 generations of 1% replacement by immigration would have to occur (Slatkin 1987).

The short-term connections between populations that we see at present may underestimate gene flow. Ehrlich and Raven (1969) summarized evidence of dispersal and breeding phenology that indicate that populations of the checkerspot butterfly *Euphedryas* are strongly localized, with little dispersal among them. Estimates of genetic differentiation, however, suggest much greater exchange (Slatkin 1987). This may have been accomplished by rare occurrences of regional extinction, with spread by individuals over many recolonized habitats. Such bouts of regional extinction and recolonization may explain the widespread homogeneity of marine invertebrate populations (e.g., Levinton and Koehn 1976), although continuing dispersal may also be a factor.

Range-extension speciation. A variant of the allopatric model that is little discussed is the *range-extension model.* Following the establishment of a new biogeographic connection, a large number of species may invade a new biogeographic region. Such corridors are often geologically temporary, so isolation may be reestablished quite soon. Alternatively, a dispersal event might bring a propagule of one or more species to a new location. This might range from long-distance planktonic larvae crossing an ocean in abundance (Scheltema 1971, 1988) to transport of unlikely dispersants on floating debris (e.g., Ingolfsson 1995), which may transport marine adults much farther than their short-lived larvae (Worcester 1994). Such long-distance invasions have been implicated in sudden appearances of fossils species in new ocean basins. For example, a corridor for marine organisms was established across the Arctic about 3.5 million years ago, connecting the North Pacific and North Atlantic Oceans (Vermeij 1991). Hard substratum invertebrates derived from the Pacific replaced nearly all of the northwestern Atlantic hard substratum biota. For example, the Atlantic *Mytilus edulis* must have been derived from the Pacific *Mytilus trossulus* (Koehn 1991). The periwinkle genus *Littorina* and the snail genus *Nucella,* among others, invaded from Pacific to Atlantic. The invasion's success was probably facilitated by a northwest Atlantic extinction, owing to glaciation (Vermeij 1991). The corridor must have been open long enough to make the specific dispersal mechanism irrelevant, because success of invasion is independent of dispersal mechanism (Vermeij 1991). It is of interest that this mechanism, which can be of major import in the composition of faunas, involves very geologically discontinuous events and produces new species of little difference from the source population. Thus, dispersal is clearly implicated in speciation (Cunningham and Collins 1998).

Parapatric speciation. The *parapatric-ecological model* argues that clinal genetic differentiation can lead to isolation among spatially contiguous populations and eventual species-level divergence in the separated populations. A geographically small ecological gradient connecting two geographic areas with rather different environments may act in effect as a geographic barrier, because strong selection may reduce gene flow across the cline. In marine habitats, points of steplike spatial change in temperature are often also the loci of geographic separation. This model, therefore, could be similar in outcome to the allopatric-dumbbell model. Apparent sharing of common alleles across such parapatric barriers can mask another pattern of fixation of rarer alleles, suggesting that gene flow has been severely reduced (Slatkin 1987). Phylogenies of genes also may be useful in mapping divergence within parapatric distributions (Slatkin and Maddison 1990).

Sympatric speciation. A variety of *sympatric speciation* models do not require geographic separation. Sympatry implies that individuals are (at least at first) physically capable of encountering one another for a sufficiently long time for mating. Ecological models of sympatric speciation usually assume strong disruptive selection, either combined with the evolution of habitat loyalty (Bush 1975) or on competitive exclusion with a subpopulation occupying a habitat patch type (Rosenzweig 1978). Like any model of speciation, breeding incompatibility must be established, but sympatric speciation requires ecological differentiation as well. As a consequence, it is necessary for the newly established daughter species to initially have genetic linkage between genes that confer breeding incompatibility and genes that regulate ecological differentiation. Otherwise, recombination will rapidly dissociate the two and speciation will not occur.

The argument for sympatric speciation also derives from evidence on current distributions. In many cases, species are found to be sympatric over wide regions. Indeed, this is the common case in sibling species of *Drosophila* that can be collected easily in the same bait traps in many localities over wide geographic ranges. Can all of these cases of sympatry have arisen originally from a process of allopatric isolation and genetic divergence?

Examples of present-day broad sympatry can be quite misleading. Co-occurrence may simply reflect a recent dispersal event of a formerly allopatrically distributed species. The apparent ecological "fit" of such a species in the present community may be misinterpreted as long-term occurrence. Co-occurrence patterns of marine snails can be misleading in this way. At present, on the east coast of North America, the periwinkle *Littorina littorea* is the dominant rocky form. *L. saxatilis* tends to occur higher in the intertidal zone. *L. littorea* first appeared in noticeable numbers in Nova Scotia in the mid-nineteenth century. It then spread southward and may still be doing so today (Kreauter 1974). But the two species of *Littorina* (there are others) are now broadly sympatric and occupy contiguous intertidal zones as if they had been sympatric for a much greater length of time.

Some cases of sympatry would be quite difficult to dismiss in this way. Carson and Okada (cited in White 1982) described pairs of species of *Drosophiella* in New Guinea and Taiwan – Okinawa, one of which breeds in male flowers, the other in the female flowers of a single plant species. Bush (1969) described the development of a series of races of the tephritid fruit fly *Rhagoletis,* based on different host occurrence and differentiation in some morphological characters. If the differentiation were genetic, and if host fidelity could be demonstrated, sympatric speciation would be a likely conclusion.

Futuyma and Mayer (1980) reviewed critically the requisites for sympatric speciation by means of host race formation in phytophagous insects. Strong disruptive selection and a host preference mechanism would be required. The Hopkins host selection principle – that adult host choice is influenced by larval conditioning – would provide a means to enhance the fidelity of incipient host races. The evidence for such host selection is very weak. No strong evidence exists to prove a genetic explanation for a host-plant association in *Rhagoletis*. Indeed, genetic variation for host-plant association generally provides a picture of a usual lack of negative correlations between fitness of one host plant versus another (Futuyma, Keese, and Funk 1995). Nevertheless, the spread of the apple maggot *Rhagoletis pomonella* to hawthorns appears to have occurred by virtue of selection related to temporal differences in larval development and may be a bona fide case of sympatric speciation (Feder and Bush 1989; Feder, Chilcote, and Bush 1990a, 1990b). In paired localities, populations on hawthorne differ from those on apple at six loci, which are mappable to three genomic regions. It is possible that premating isolation evolves owing to pleiotropic genes that affect host choice and simultaneously cause temporal displacements in life histories (Etges 1998).

These general principles can be extended to other types of proximate but distinct habitats where local differentiation occurs, associating a different morph, respectively, with each habitat. In butterflies, for example, wing pattern and color polymorphism can readily develop within a single species, as long as there are some adjacent habitats. In the passion-vine butterflies of the genus *Heliconius, H. erato* and *H. himera* maintain their separateness, despite complete interspecies compatibility when matings are forced (McMillan, Jiggins, and Mallet 1997). Mate choice is associated with color pattern: Like prefers like. In turn, the color patterns are associated with vegetation types (wet and dry forest).

Ecological speciation. Imagine a case in which a population lives in a bimodal habitat. If the two habitats were isolated, natural selection would in all likelihood yield two morphologically distinct populations. Now suppose that the divergence creates two populations with strong philopatry. This might be related to the steep drop in behavioral performance (e.g., feeding on live prey) if individuals of one population strayed into the other's optimum habitat. Such isolation might be the basis for further separation, such as separated breeding sites. Speciation would be under way.

Crucial to this mechanism is a reciprocity of performance. Individuals of one population must perform poorly in the subhabitat occupied by the other population (Schluter 1996). Even better, crosses between the two populations might produce phenotypes that are not efficient in either subhabitat. This might select for premating isolation. Thus, even if there is some connection between the two subhabitats, speciation might still develop.

This model is a hybrid between the parapatric and sympatric models. Indeed, the distinction between the two breaks down here. At first, one might say that this a sympatric speciation model, but later, parapatry might come into play.

This model should work well for species whose individuals can choose microhabitats that maximize growth and reproduction. Sticklebacks represent a tantalizing but ambiguous case (Schluter and McPhail 1993). Many lakes contain so-called benthic forms and limnetic forms. Limnetic forms are smaller and streamlined and adapted to movement in the water column. Along with overall shape, gill rakers are longer and better suited for straining plankton than are the shorter, sparser rakers of the benthic form. The benthic form is deep in shape, which is a suitable form for maneuvering in complex habitats, as opposed to cruising. The presence of both forms in many lakes begs the question of the origin of the divergence. Are different lakes each the site of a miniradiation, driven by disruptive selection? Or did the two morphs arise alone by strong directional selection and have they occasionally colonized the same lakes? In any event, it appears that natural selection is predictable and reproductive separation inevitable. A study of several British Columbian lakes demonstrated that benthic forms crossed more successfully with other benthic forms, irrespective of whether they came from the same or from different lakes; the same result obtains for the limnetic form (Rundle, Nagel, Boughman, and Schluter 2000). Thus, those that evolve in ecological isolation mate more infrequently than those who evolve in similar ecological circumstances. In effect, speciation is being driven by natural selection in a spatially heterogeneous environment.

Many communities show characteristic habitat partitioning among species with limited resources. Rocky shore zonation of dominant forms is a classic for marine systems, and zone boundaries are often regulated by interspecific competition (Levinton 1995). In sediments, stratification is often found for infaunal marine invertebrates; dominant species occupy different levels below the sediment–water interface, a probable result of competition for space (Levinton 1977; Peterson and Andre 1980). Could such structure be intimately related to speciation? We have one excellent example of this in *Anolis* lizards of the Greater Antilles. Williams (1972) pioneered the ecological study of such species assemblages and found a characteristic four-species complex. It is possible that the ecologically distinct species arose independently and colonize new geographic regions, but seek the microhabitat which is best suited to them. But phylogenetic analysis indicates that the assemblage of four species with contiguous hides diverged independently on each island, producing apparent predictable repeat situations where speciation paralleled ecological divergence (Losos, Jackman, Larson, Dequeiroz, and Rodriguez-Schettino 1998). Thus, adaptive radiation in similar environments can overcome historical contingencies to produce strikingly similar evolutionary outcomes.

Ecologically driven speciation is a case in which natural selection and speciation may be coincidental, much like sympatric speciation. Indeed, as mentioned above, the two processes are not readily discernible.

Evidence from current geographic distributions: does it solve any problems? The ubiquitous presence of geographic variation and the common ability of workers to extrapolate intraspecific variation within polytypic species to interspecific divergence is the usual justification for the importance of allopatry (or parapatry) in speciation (Mayr 1963). The evidence garnered in recent years on chromosomal races of small mammals and patterns of strength of premating isolation suggest that allopatry followed by divergence of isolates is a common mode of speciation. In sister species, premating isolation appears to be accentuated when they reestablish contact (Coyne and Orr 1989). The extrapolation of geographic races to species with contiguous distributions is powerful evidence of vicariant allopatric speciation, as it is difficult to imagine another explanation for a present-day distribution of a series of closely related species with contiguous ranges. But it would be difficult to use such evidence to distinguish between strictly allopatric and parapatric models. Divergence will emerge if the geographic selection gradient is steep and if dispersal is ineffective (e.g., Barton 1983; Endler 1977). Most hybridizing zones are probably quite ancient, as they connect genetically divergent species. As a result, current distributions of such zones may tell us little about the origin of genetic divergence. Dispersal may blur and widen hybrid zones, but this doesn't necessarily demonstrate any particular process behind the original evolution of isolation (Barton and Hewitt 1985).

In many cases, it will be difficult to distinguish between parapatric differentiation and geographic isolation. After all, areas of steep geographic environmental change may also isolate populations physically on either side of the steep ecological transitional zone. Such an ambiguity shows up well in the case of killifish differentiation along the east coast of the United States. Powers and Place (1978) found a strong north–south cline in an allele at the heart-type *LDH-B* locus of *Fundulus heteroclitus,* a diminutive estuarine and open marine bottom-feeding fish (Figure 3.13). The *LDH-B-b* allele is common in colder waters, whereas the *LDH-B-a* allele dominates in warmer southern habitats (Place and Powers 1979). Reaction velocities for enzymes derived from *LDH-B-b* allele homozygotes were higher at lower temperatures (10°) than for enzymes derived from homozygotes for the alternative allele (Figure 3.14).

Adenosine triphosphate (ATP) levels were also correlated with *LDH-B* genotype; concentrations were found to be lower in the *LDH-B-a* (southern) homozygotes.

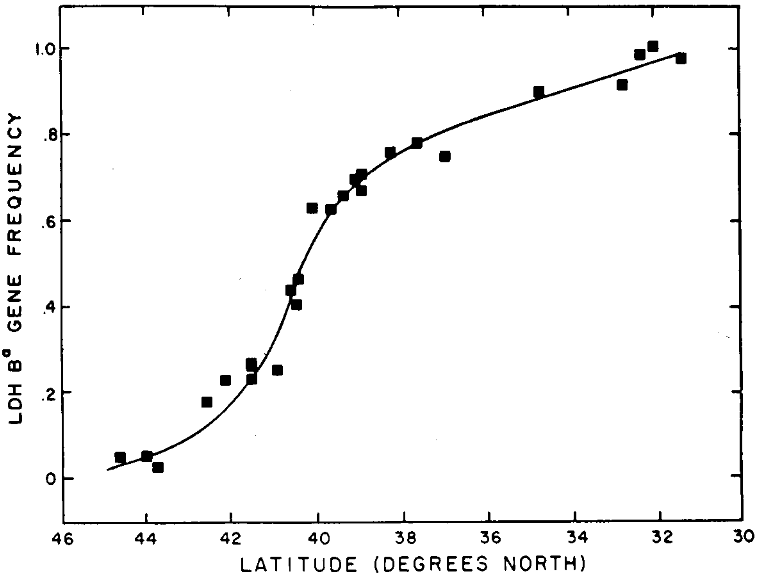


Figure 3.13. Geographic variation in an allele at the *LDH-B* locus of the killifish *Fundulus heteroclitus.* (After Powers and Place 1978.)

ATP is an allosteric modifier of hemoglobin and therefore must affect muscular oxygen supply. At 10°C, the critical swimming speed (CTS – speed at which fish are exhausted) was 3.6 body lengths/sec^{-1} for homozygotes for the *LDH-B-a* allele (cold), whereas CTS was 4.3 for homozygotes for the *LDH-B-b* (warm) allele (DiMichelle and Powers 1982). The difference disappears at 25°. The low-tempera-

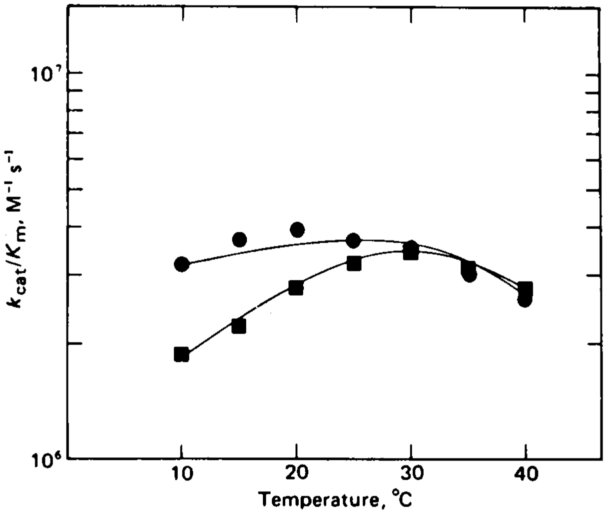


Figure 3.14. Comparison of interpolated and measured estimates for LDH k_{cat}/K_m at pH 7.5 for two genotypes of the killifish *Fundulus heteroclitus.* (After Place and Powers 1979.)

ture advantage of the *LDH-B-b* allele seems related to the elevated correlated concentrations of ATP that reduce oxygen affinity and allow easier delivery of oxygen to starved tissues. This seems to be a mechanism to accelerate the activity of a cold-water fish, to compensate for its otherwise poikilothermic faithfulness to a fixed temperature-metabolism-activity relationship. Such latitudinal compensation is common for physiological characters of coastal species in latitudinal gradients (Levinton and Monahan 1983). If the northern population could not swim faster at the same low temperature, then fish would spend much of the year in a moribund state, unable to gather food or mate. But this increased activity must have a cost, leading to progressive adaptation for reduced acceleration in increasing temperatures.

The latitudinal variation in killifish allozyme frequencies may therefore be explainable by natural selection, despite the potential for coastal dispersal that would homogenize allele frequencies. Most notable is a step-cline in frequencies in New Jersey waters, marking a transition between northern and southern populations. Does natural selection maintain these clines? DiMichelle and Powers's results for *LDH* suggest that this might well be so, but another important element enters the picture. Mitochondrial DNA RFLP markers show dominance by two different haplotypes in the northern and southern populations (Gonzalez-Villàseñor and Powers 1990), although some outliers of the southern populations can be found in isolated pockets in the north. Estimates of population mixing using unique alleles and construction of standard trees both support the hypothesis that isolation between these two major populations is sufficient to have allowed differentiation owing to genetic drift (Brown and Chapman 1991). Although natural selection probably imposes an overprint, isolation clearly is a major factor in the steep cline off the New Jersey coast. Thus, mtDNA markers highlight the ambiguity between gene flow and natural selection.

A similar difficulty in conflating selection and gene flow was discovered for the marine mussel *Mytilus* in the Kattegat, which connects the Baltic Sea and the North Sea. There are strong clines at five allozyme loci over a distance of a few kilometers, which is surprising in light of the dispersal capabilities of *Mytilus* planktotrophic larvae. Thus, natural selection was thought to cause high mortality as inappropriate genotypes moved along the Kattegat. But subsequent work revealed that all strong multilocus clines are not the result of strong selection but a result of isolation and speciation (Koehn 1991). Thus, the Baltic Sea population is *Mytilus edulis* and the North Sea population is *M. trossulus*. A similar zone of contact can be found from the Spain–France border to parts of the British Isles between *M. edulis* and *M. galloprovincialis*. Here, hybridization is extensive and hybrids are not lower in fitness, as indicated by the extensive backcrossing observed. The hybrid zone appears to be maintained by selection in favor of *M. galloprovincialis,* which is counterbalanced by massive immigration of *M. edulis* recruits (Gardner 1994).

The pattern we see suggests the following: Marine speciation is an accidental process that has little or nothing to do with accelerating evolution in adaptive traits. Rather, the zones of contact we see appear to be secondary intergradations. The primary processes of natural selection appear to determine the primary matrix within which adaptive evolution occurs.

Probably the most elegant evidence for the continuity of polymorphism, polytypism, and speciation can be found at stable biogeographic boundaries. As mentioned above, coastal marine biogeographic zones are often broken up by isolation, promoted by separated current systems. The southern part of Florida, although having a rather complex history, proves to be a major biogeographic break, separating Gulf of Mexico faunas from those on the Atlantic coast. Species ranging from coastal marine invertebrates to coastal terrestrial species (Figure 3.15) have either species breaks or strong genetic differentiation without speciation, as registered by RFLPs (Avise 1992, 1994). The marine species barrier is probably explained in the main by the separation of the Gulf Stream from the southeast coast of Florida as it moves northward. One gets the impression that different species have reacted in complex ways to the barrier, so the degree of differentiation varies accordingly. A similar pattern of differentiation can be gleaned from freshwater fish distributions in adjacent southeastern United States watersheds (Avise 1992).

Major biogeographic barriers, such as Point Conception, California, and Cape Cod, Massachusetts, are loci of temperature change and separations of currents that might isolate populations. RFLP data can illuminate the degree of isolation, assuming that the differentiation is related to stochastic differences on either side of the isolating barrier. Over periods as short as decades, these barriers may be transitory. For example, El Niño years bring warm surface water to the eastern Pacific, and a breakdown in the previously established current structure causes warm water to

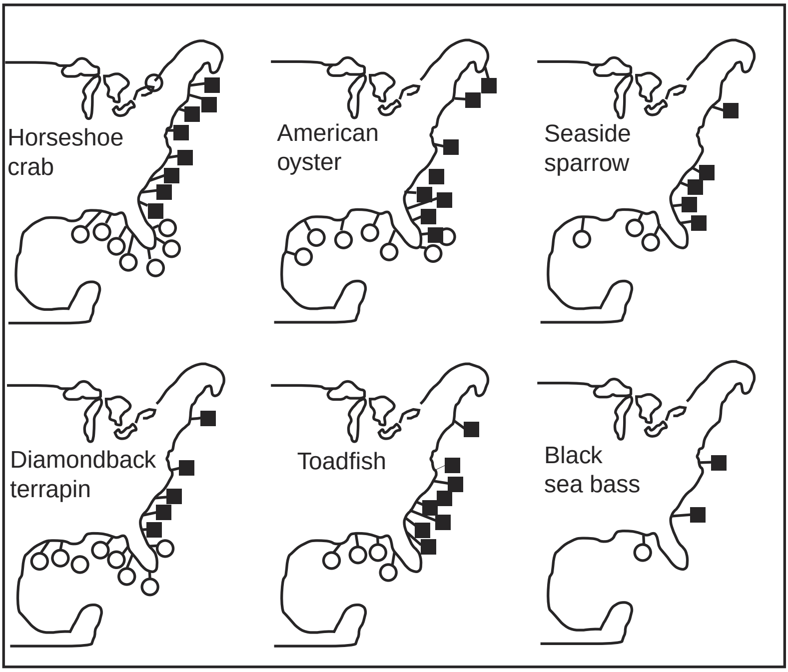


Figure 3.15. Geographic distribution of mtDNA genotypes of maritime taxa across the southern Florida biogeographic break. (After Avise 1992.)

move rather freely from the south to the north of the normally isolating Point Conception, California. Therefore, warm-water species and their genes may be carried northward during such episodes (Alexander and Roughgarden 1996). RFLPs are useful markers of the stability of such barriers. Some coastal species, such as tide pool harpacticoid copepods, are less prone to move great distances successfully, and surprising levels of differentiation at the sequence level were found on either side of Point Conception (Burton and Lee 1994).

DNA sequence–based evidence for isolation may reveal evidence for selection between isolated populations. Karl and Avise (1992) found a strong boundary marked by nuclear RFLPs between two populations of the eastern American oyster *Crassostrea virginica*. Previously, homogeneity of allozyme frequencies across this newly discovered barrier were thought to represent evidence for widespread gene flow, but instead it became clear that stabilizing selection likely maintains similar allozyme allele frequencies on either side of a strong isolating barrier.

The predominance of allopatric or parapatric speciation leaves open the geographic aspect or the dumbbell-peripatric distinction drawn above (omitting the problem of genetic revolutions). Is most speciation a budding process, or does it occur by geographic separation well within the range of an extant species? It is probable that both modes are common. The evidence mentioned above for the butterfly genus *Heliconius* suggests that polytypism can develop into speciation, a process consistent with the dumbbell and parapatric models. Many newly derived species, however, are buds on the edge of the range of extant species. This has been documented in some plants (Gottlieb 1976; Lewis 1973; Stebbins 1983a). Diploid newly derived species of *Clarkia* in California occupy ecologically marginal habitats and are characterized by numerous chromosomal structural differences that substantially reduce the fertility of hybrids. The daughters are competitively inferior to the parent species, even on the sites where the newly budded species live. Speciation by budding in plants is facilitated by the possibility of selfing in the neospecies (see Gottlieb 1976).

A more strictly genetic mechanism of parapatric speciation has been suggested by White (1968). The *stasipatric* model surmises that fixation of a chromosomal rearrangement in a small population can occur within the range of a larger species population. The rearrangement thus spreads from the center and partially displaces the surrounding ancestral population. The parapatric contact between the spreading nascent species and the surrounding population is therefore maintained by strong heterozygote inferiority (Lande 1979a); otherwise, extensive gene flow and introgression with the surrounding population would ensue. Meiotic drive, or biased survival of gametic types, would enhance the spreading potential of a novel chromosomal variant.

Futuyma and Mayer (1980) pointed out that cases of stasipatric speciation cited by White (1968) are consistent also with an allopatric model of local fixation and deme spread. Worse than that, they noted that all cited cases of stasipatric speciation fail to demonstrate extensive reproductive isolation. Such isolation would probably not be established by a single fixation of a chromosome rearrangement as signficant gene flow could still occur. This hardly supports the possibility of expanding fronts of incompatibility suggested by White (1974).

Genetic architecture of speciation. Templeton (1981, 1982) has classified speciation mechanisms within a genetic context. He defines two overall processes. *Divergence models* involve the gradual evolution of differences between populations living in ecologically distinct habitats. Divergence can occur among completely isolated populations (adaptive divergence) or along a cline if gene flow is restricted. Isolating barriers between incipient species evolve in a continuous fashion and may reflect only divergence in response to selection in different environments, or to genetic drift. The accumulation of genetic differences increases the probability of fixing differences that would produce sterile hybrids if contact between the isolated populations was reestablished. Templeton argued that adaptive divergence is the mode of speciation. By contrast, *transilience* models drive speciation from a discontinuity in which a selective barrier is overcome by other evolutionary forces such as drift. The founder principle of the peripatric hypothesis of Mayr would apply here, as would the origin of chromosomal incompatibilities among populations via inbreeding and drift. Because natural selection could operate even in cases in which transilience mechanisms are in operation, a sharp distinction between the two overall modes is not possible.

Templeton also distinguishes among different genetic architectures that might differentially affect the evolutionary fate of populations placed under similar selective and stochastic forces. Type I consists of traits that are controlled by many genes of subequal effect. Type II architectures control traits by only a few genes with large effects, modified by genes with small effects.

The genetic architecture of a trait may also reflect the selective regime during the evolution of the trait. Rapid evolution owing to intense directional selection might favor the predominance of type II architectures in trait determination. Under strong selection, alleles with relatively large phenotypic effects would be shifted strongly in frequency. By contrast, slow divergence might favor type I architectures.

The genetic revolution hypothesis of Mayr is based on several assumptions about the genetics of colonizing populations and the degree of adaptive interaction among genes. The *founder effect* hypothesis asserts that founding populations are extremely biased relative to the genetic content of the source population. Intense selection is thought to break up coadapted gene complexes and to strongly alter the genetic architecture of the newly derived species. These points can be examined from both theoretical and practical points of view.

Before proceeding, I must emphasize that species do commonly originate as buds at the periphery of other species of large geographic extent. Mayr (1954) cited many examples of divergent bird populations on small islands, as compared to nearby geographically widespread mainland or large island populations. The fiddler crab *Uca panacea* arose in a small area and was derived from the much more widespread *U. pugilator* (Salmon et al. 1978). Such a geographic configuration is necessary for peripatric speciation, but not sufficient to fulfill the expectations of the model, as local selection pressures might enhance differentiation in the absence of a genetic revolution. Indeed, we might expect that geographically peripheral areas will be ecologically extreme and promote strong natural selection, which may result in speciation.

Founder effects are unlikely to be very important in colonizing populations. The reduction in overall genetic variability relative to a source population is likely to be modest even in founding groups of ten or fewer (Lande 1979a). Even with continuous brother–sister mating, heterozygosity decreases only 19% per generation. Intense inbreeding of this sort would be unlikely in most animal populations but could occur in facultatively autogamous plant populations.

For morphological traits, our conclusions about the reduction of variance presume that additive (among-allele) variation is the only important factor in the determination of a trait. Under this assumption, even a few individuals still carry most of the allelic variation of the population. Some experiments on bottlenecked populations require some reconsideration of the assumption. Bryant, McCommas, and Combs (1986) passed populations of the housefly *Musca domestica* through bottlenecks as small as one pair. Surprisingly, the additive variance for a variety of traits increased in the bottlenecked lines. These results cannot be explained by a simple additive model, which would predict a loss of additive variance. It is possible that the traits are explained by more complex genetic relationships, such as dominance of certain alleles, that are lost through the bottleneck. This would telescope the variance, but Bryant et al. argued for other effects as well. In any event, these results reduce any hope for the founder effect, except with regard to a crucial point made by Mayr: the possibility that intense selection might be operating on a novel rearrangement of genetic relationships. The sheer loss of alleles still seems unlikely.

Studies of Hawaiian Drosophilidae fail to demonstrate strong genetic changes despite rampant speciation. If founder effects were important, they would be evident throughout the genome. Although gene substitutions are common, there is no evidence of reductions in heterozygosity in more derived species, nor are there even significant differences in variability between most closely related species (Carson, Hardy, Spieth, and Stone 1970; Carson and Kaneshiro 1976; Rockwood et al. 1971). Carson and Templeton (1984) would argue that such species did lose variability, but a subsequent expansion coincided with a large population increase following speciation. They did not explain how this would accommodate the widespread sharing of alleles found in sister species. Even severe and relatively sudden bottlenecks, as registered by loss of a large proportion of mtDNA haplotypes, may not result in any significant reduction of allozyme heterozygosity or even genetic differentiation among sites where bottlenecks have occurred (Ovenden and White 1990). It is possible that some allozymic phenotypes in separate species arose by mutation and convergent evolution.

Although changes are not radical, the classic work of Ayala et al. (1974) demonstrated that sibling species often show allelic substitutions for a large part of the allozyme loci surveyed. But in subspecies, semispecies, and within-species populations, the dominance of shared alleles is quite clear. It may be that sibling species are sufficiently separated in time such that drift causes the fixation of large numbers of alleles over many loci.

For several decades, laboratory strains of *Drosophila* have been established from a single gravid female with only rare instances of the subsequent development of interstrain incompatibility. Cases of the evolution of laboratory reproductive incompatibility generally involve intensive disruptive selection (Thoday and Gibson 1962). Carson and Templeton (1984) argued that the failure to see speciation in bottlenecks may relate to our consistent use of species with particular genetic architectures. They argued that species in nature commonly have gene complexes (major genes with modifiers) that would be more easily subject to rapid change in a laboratory culture. But there is no clear evidence that such differences in genetic architectures exist.

Even if founding populations are not likely to be strongly unrepresentative of source populations, the question of breakup of coadapted gene pools is a problem still equally applicable to more central populations and peripheral colonizing populations. This would be especially true if even central parts of a species range are broken up into small isolated demes. Despite many strong claims pro and con, we still know little of the degree to which coadapted gene pools exist.

Maynard Smith (1982) focused the problem by defining two alternative hypotheses about genetic organization. It is useful to speak of such organization in terms of its conceivable effects on developmental processes. The null hypothesis argues that no genetic organization is developmentally relevant on a scale larger than the gene family (a group of closely linked genes with controlling sequences). The alternative hypothesis would argue that large-scale organized structures of the genome are significant in development.

On the grossest scale, the null hypothesis is well supported by available data. The absence of linkage among loci of related functions is quite common (discussion in Kimura 1983). In *Drosophila subobscura,* where paracentric inversion polymorphisms occur on all autosomal arms, no effects of polymorphism on morphology can be observed. In general, the degree of absence of such organization is surprising (Turner 1967). Despite some theoretical expectations (Franklin and Lewontin 1970), the genome does not usually congeal into closely linked complexes of coadapted alleles. Recombination apparently is a more potent force than selection for such linkage disequilibrium, perhaps as the result of reversing selection pressures.

Although gross chromosomal organization seems unlikely, smaller-scale organization nevertheless exists. First, as mentioned above, nonhomologous chromosomes may join at sites of common gene families during transcription. This is a form of large-scale organization that might be strongly disrupted with changes due to recombination. Second, many sets of genes with related function are spatially contiguous. This is especially true of many multigene families, where the repeats occur in tandem arrays (e.g., the chorion genes of silkworms; Kafatos 1983). One cannot be sure whether this is just a function of history (e.g., unequal crossing over) or preservation by natural selection, as in a supergene. If homogenization processes such as gene conversion have a positive effect by “correcting” mutations, the maintenance of proximity of genes of related function might be adaptive. The same can be said for many linkage relationships among allozyme loci in mammals that are quite ancient (O’Brien and Nash 1982). The bithorax series is another example of a long-lived complex of closely linked genes. It is possible that this may relate to transcriptional order in development, but the linkage between gene order and developmental order is by no means universal. Finally, some cases of close linkage of enzyme loci with similar function or with regulatory loci are known. At the scale of the gene neighborhood, linkage disequilibrium seems to be quite important (see Aquadro, Desse, Bland, Langley, and Laurie-Ahlberg 1985).

Genetic drift can be shown to promote among-population divergence. Experimental studies with *Drosophila* demonstrate that divergence in chromosome inversion frequencies and mating success is more substantial when populations are started in low numbers, or when they are passed through bottlenecks, relative to those started and maintained at high numbers (Dobzhansky and Pavlovsky 1957; Dobzhansky and Spassky 1962; Santibanez and Waddington 1958). The increased phenotypic variance must increase the probability that natural selection will move the average phenotype of a population to a new adaptive peak, as variation available for selection is increased. Charlesworth, Lande, and Slatkin (1982) noted that these experiments usually involve starting populations derived from interpopulation crosses, and there is good evidence that the stocks differed in background genes that interacted in fitness with genes contained in inversions. The relevance to processes in founder populations, which ought to be derived from a single locality, is therefore unclear. Divergence in the subpopulations might involve a resorting of genes from the respective local stocks to reestablish favorable combinations of modifiers.

The requisite of genetic revolutions for speciation is based on the premise of species integrity. Because he believes in the "unity of the genotype," Mayr (1963, chapter 4) requires a mechanism to break up the coadapted gene complexes that supposedly constrain evolutionary change within the normal geographic range of a species. Although there is ample evidence of intergene interactions, particularly epistatic effects on fitness of genes segregating in populations (see Charlesworth and Charlesworth 1975; Templeton 1979), there is no reason to believe that these phenomena would prevent selection from operating to change a trait, though we would certainly not expect wings to sprout on the backs of mice. Single founder effects are much less potent in enabling extensive evolutionary change by drift (Lande 1980b) or natural selection (Hill 1982). It is true, however, that a founding population could more easily be dominated by genetic drift, relative to selection. Therefore, changes that might be accomplished in just a few generations by a combination of strong drift and natural selection would be focused in the sort of founding populations discussed by Mayr and by Carson and Templeton. But one would also expect drift at some neutral loci (e.g., allozymes), and there is no evidence for this in Hawaiian drosophilids, the prime case used by Carson and Templeton. The longevity and variability of large populations would promote both divergence and reproductive isolation.

In summary, the geographic aspect of the peripatric model is plausible. Populations may indeed usually bud off from the main range of a species. Intense selection and genetic drift may combine to cause divergence, but longer-lived large peripheral populations would be more potent than small ones in this regard. The concept of genetic revolution seems without foundation. Moreover, many of the changes occurring as the result of selection and drift at the periphery of a species range could just as easily occur in isolated demes well within the range of a species. Most important, the probability of a fitness peak shift across a deep valley is very low in a small peripheral population. Given its likely short life span, successful speciation would have to be very rapid. The peripatric model is therefore probably applicable to the degree that peripheral areas are ecologically distinct or can guarantee isolation.

Some models involving transilience mechanisms are supported by distributional evidence. *Polyploidy* is widespread in plants and is known to occur in animals (Ohno 1970; Stebbins 1971). The occurrence of polyploidy is usually followed by the evolution of gene regulation mechanisms that effectively diploidize the population. Doubled occurrences of genes are regulated in various ways to resemble species of diploid origin (Leopoldt and Schmidtke 1982).

Because chromosome doubling usually is associated with hybridization, the effects of doubling are difficult to uncouple from those of hybridity and recombination. It is the latter that are thought to be of importance in evolutionary potential (Levin 1982). Chromosome doubling has some immediate ecological consequences. DNA content in plants is positively correlated with mitotic cycle time and cell size. Polyploids usually have slower development, delayed reproduction, longer life time, larger seeds, and lower reproductive effort (Levin 1982). Polyploidy can conceivably be directly related to the rate of morphological evolution and propulsion into new ecological milieus. Polyploidy is more common among annuals than perennials.

Although polyploidy may be a source of new morphological variance, it is important to remember the common dependence of flowering plants on apparently closely matched insect pollinators. Hybrids intermediate in form between parent species, or of highly changed form, even when autotetraploid, may be thrust out of the range of pollinator service. Stebbins and Ferlan (1956) noted this for *Ophrys murbeckii,* a hybrid derivative from *O. fusca* and *O. lutea.* In this genus, bees pollinate by pseudocopulation, based on the hairs, color, and form of the labellar surface. The two parent species are distinct, whereas the hybrid is intermediate in all respects, except in certain characters such as the small size of the labellum. Stebbins and Ferlan concluded that hybrids are being formed all of the time but that most do not reproduce for lack of a pollinator. The ones that do reproduce must have some pollinator capable of servicing the flowers. When a bee pollinates a hybrid, segregating progeny will be produced and strong directional selection will ensue to adapt the plant to the new pollinator; otherwise, extinction will follow.

Intraspecific homogeneity in nucleotide sequence is found in members of multigene families, ranging from a few (e.g., some transposable element families in Drosophila) to 100,000 in number (e.g., the *alu1* family in humans). This homogeneity stands in contrast to the common situation of interspecific heterogeneity. This pattern reflects the processes of unequal crossing over, gene conversion, and duplicative transposition (Arnheim 1983; Dover 1982).

The phenomenon of gene family homogeneity is spread over many taxonomic levels. In some cases, homogeneity is found only in members of a single species. This is true for families of noncoding sequences, introns, and other cases in which the DNA sequence has no apparent function. Homogenization must proceed rapidly with respect to the rate of speciation. Where functional constraints appear to be important, homogeneity can be interspecific and may unite several related species. The varying degrees of interspecific differentiation can be mapped onto a cladogram like any other set of characters.

Divergence at different taxonomic levels can be seen in sequence divergence in species of cereals (Poaceae; see Flavell 1982). The haploid sizes of species of Poaceae fall in the range of 3.6 to 8.8-picogram DNA and are over an order of magnitude larger than that of *Drosophila.* Over 75% of the DNA consists of non–coding repeated sequences, which can be divided into families, either clustered in tandem arrays or spread on several nonhomologous chromosomes.

In the species of wheat, *Aegilops squarrosa, A. speltoides,* and *Triticum monoccum,* nearly all of the highly repeated families are identical between the two species of *Aegilops.* About 2% to 3% of the genome of *A. speltoides* consists of families not found in the other two species, but most of the repeated DNA families are common to all three species. The use of restriction endonucleases reveals the presence of species-specific subfamilies that have evolved since the species diverged. Thermal stabilities of reannealed sequences between wheat and other species show a progressive increase in degree of dissimilarity as taxonomic distance increases (Smith and Flavell 1974).

The degree of meiotic chromosome pairing reflects the increasing sequence divergence in the multigene families of these species. As taxonomic divergence increases, the frequency of chromosome pairing and chiasmata formation decreases. This may be related to increased divergence due to differential gene family homogenization in geographically separated groups. This might result in sterility of hybrids if the populations reestablish contact.

Processes of gene homogenization and duplication may be sufficiently different in geographically isolated species to inhibit chromosome pairing between hybridizing genomes and thus cause reproductive isolation and speciation. The correlation between multigene family divergence and decrease of chromosome pairing may, however, lack a causal connection. It is possible that divergence in single-copy genes also occurs and is the primary source of chromosome pairing failure during meiosis. By contrast to Flavell's (1982) results for *Aegilops* and *Triticum,* Rees, Jenkins, Seal, and Hutchinson (1982) reported no differences in chiasmata formation in intraspecific versus interspecific crosses among species of the cereal genus *Lolium.* Fertile hybrids can be generated despite a difference of 40% in nuclear DNA. In crosses between the more distantly related *Festuca drymeja* and *F. scaricea* ($2N = 14$ in both species, but 50% difference in nuclear DNA), chiasma formation occurs at low frequency. Nevertheless, a surprising amount of pairing occurs. Pairing at pachytene is nearly complete despite DNA differences among chromosomes ranging from 25% to 42%. Pairing among larger chromosomes can be accomplished by means of loose ends or loops. Failure of pairing is more prominent on shorter chromosomes. Thus, extensive divergence in DNA content may exert only modest effects on compatibility, but the effect may be sufficient to prevent crossing among populations with divergence in multigene or sequence family size. The relative contribution of genic and overall chromosomal compatibility to divergence is an open question, except in the many cases in which chromosome divergence is apparently absent.

A similar possibility of divergence and incompatibility has been mentioned above for transposable elements involved in hybrid dysgenesis (Kidwell et al. 1977; Rubin, Kidwell, and Bingham 1982). One or more unique transposable elements might spread in an isolated population. The probability of spread will depend on the reduction of fitness in crosses between infected and noninfected animals, relative to the infection rate. In the P system, takeover may have taken only a few decades (Kidwell, Novy, and Feely 1981). This might result in the eventual accumulation of sufficient transposon family differences to affect postmating isolation, should the population be united with a conspecific but previously separated population. Interstrain incompatibility similar to hybrid dysgenesis has been observed in other species, but it is not necessarily due to the same underlying mechanism.

Current evidence casts some doubt on the role of transposable elements in speciation. This hypothesis has been proposed on both empirical (Bingham, Kidwell, and Rubin 1982) and theoretical (Ginzburg, Bingham, and Yoo 1984) grounds. Hey (1988) examined differences among semispecies of the *Drosophila athabasca* group, and between this group and *D. algonquin.* In contrast to known divergence in allozymes, inversions and morphology, there were no detectable differences in the presence of dysgenic transposable elements.

The theoretical treatment of Ginzburg et al. (1984) suggests that the drop in fitness imposed by crosses with dysgenic strains would select for avoidance of hybridization and would lead to the evolution of premating isolation, further reinforcing the speciation process. The details of at least the known dysgenic P-M and I-R strains suggest a different interpretation (Hey 1987). First, dysgenic crosses are not reciprocal, and hybrid females with limited fertility may backcross to the maternal population; the progeny will not be dysgenic but will carry transposable elements and would inherit the cytotype associated with the elements. The transmission of elements via hybrid and partially hybrid females would destabilize the hybridization barrier. The barrier would only be stable if complete sterility were the result of crosses with strains carrying the elements. Even in this case, Hey (1987) noted that functional elements are lost rapidly, making them important as a barrier for very brief periods. As soon as individuals with dysfunctional elements appear, then hybridization can occur. The time period would appear to be less than 30 years, in the case of the P-M system of *D. melanogaster.* This brief window of opportunity may explain why Hey failed to find evidence for the action of transposable elements in speciation in *Drosophila.* It has been suggested that mutation rate might be accelerated in interspecies hybrids, but Coyne and Orr (1989) examined hybrids within the melanogaster species group and found no difference, relative to intraspecies crosses. Excision rates were higher in hybrids, indicating accelerated repair. Overall, however, there was no support for a specific mechanism that would relate transposable elements to speciation.

Isolation need not inevitably result in interpopulation incompatibility after long periods of isolation. Stebbins (1983a) cited cases of isolation among plant species populations for several million years with no apparent loss of reproductive compatibility.

In summary, we can and do find many examples where transilience mechanisms appear to contribute to reproductive isolation between species. Polyploidy, a mechanism that is rampant in plants, is especially important. Nevertheless, the balance of the evidence militates against transilience mechanisms as the major motor of speciation, especially in animals. The dominant pattern of contiguity of geography, increasing genetic differentiation, and finally speciation, further heightened by enhanced evolution of premating isolation mechanisms on contact of separated species, is strikingly clear. Geographic isolation or reduced gene flow, in combination with localized selection forces, appear to dominate the origin of species and differentiation of traits, with a small addition of sympatric-ecological and transilience mechanisms.

Transspecific Stasis

As allozyme and chromosomal techniques have been applied to natural populations, it has become apparent that extensive speciation occurs with little morphological change. This is ironic in the case of the mammals, because morphological evolution in this group is believed to be rapid, relative to others (e.g., Stanley 1979; but see Gingerich 1983, and chapter 6). The rapidity may be coincidental and morphological evolution may be related to adaptive shifts rather than genetic mechanisms. This is best illustrated by the hundreds of genetically distinct races of various species of mice, accompanied by little morphological change. Consider further the rampant speciation of the genus *Peromyscus* with little morphological divergence (Kurtén 1981). If frogs change little in adult morphology, it may be that natural selection promotes little divergence.

It might be argued that cases of evolution of reproductive isolation in the absence of morphological divergence might be restricted to a small group of taxa with restricted dispersal and chronically small population sizes. Common cases of speciation without significant morphological divergence, however, are far more widespread. Morphologically nearly identical species, or *sibling species,* have long been known in groups such as *Drosophila.* Careful examination of many other groups presents a similar overall picture (see Mayr 1963, chapter 3).

Investigations of marine species in recent years have greatly altered the traditional picture of widespread single species. Networks of nearly identical sibling species have been found in most groups of marine invertebrates (Knowlton 1993). The fiddler crabs of eastern North America are a useful example (Salmon, Ferris, Johnston, Hyatt, and Whitt 1979). Speciation in most of the temperate and in some of the subtropical North American species has occurred without significant morphological divergence. Species recognition is usually futile without a careful study of male mating behavior, which often differs among species (Crane 1975). In the species pair *Uca speciosa* and *U. spinicarpa,* morphology is identical despite allozymic difference indicative of an approximate 12 million years' divergence time ($D = 0.7$). *U. pugilator* and its closest relative, *U. panacea,* are distinguishable only by virtue of a different waving display and slight color differences. Overall, the ca. 100 species of *Uca,* spread throughout the temperate and tropical world, are generally similar in form.

In marine polychaetes, previous notions of broad-ranging single species have been supplanted by demonstrations of large numbers of morphologically identical species. The genus *Ophryotrocha* (Dorvilleidae) has been shown to consist of a very large number of sibling species of varying life history but strong morphological similarity (Åkesson 1973). The polychaete *Capitella capitata,* previously thought to be a cosmopolitan opportunistic species, is now known to consist of a large number of sibling species (Grassle and Grassle 1974). Similar cases have also been discovered in marine mussels (Seed 1978). The blue mussel, *Mytilus edulis,* was thought to be a widespread species but turns out to be a complex of morphologically similar sibling species (e.g., Koehn, Hall, Innes, and Zera 1984, Koehn 1991). Such discoveries have also extended to forms formerly thought to be ecotypes, as in corals of the genus *Acropora* (Knowlton et al. 1997). This case is quite interesting, as it tells us that we have little intuition in distinguishing between morphologically plastic responses to environmental change within a species and true species differences!

We are well on the way to appreciating terrestrial species diversity, but marine invertebrate diversity is probably far from being understood. The sort of scrutiny long in vogue for terrestrial mammals and insects is only in its infancy for marine species. One problem with this ignorance is that morphological variation ascribed to a single polytypic species might instead be the sum of variation of several sibling species. My guess is that this problem is not limited to any particular marine realm, but surely it must be a greater problem in the diverse tropics.

Although we have uncovered many sibling species complexes, a larger pattern of general constancy of form is apparent in many groups of organisms. Many genera are quite ancient and consist of groups of species whose overall form has deviated little from a common morphology (Wake, Roth, and Wake 1983). Morphological constancy goes beyond sibling species; it may be a mistake to think of speciation as bimodal in its generation of morphological divergence. The vast majority of speciation events probably beget no significant change.

If, as in most other examined cases, many morphological traits have sufficient heritability to allow extensive change during phyletic evolution or speciation, it follows that some conservative, and speciation-transcending, force preserves *transspecific stasis*. Stabilizing selection is the most likely candidate for such stasis. The transcendence of form beyond the species level has long been recognized. Rensch (1959, p. 93), for example, noted: “It is conspicuous that most such persisting types are not immutable species, but persistent genera, the changing species of which preserve a certain type of adaptation.” One might add that the generic-level distinction is probably made on the basis of a preconceived notion that the genus level is an adaptively significant threshold of morphological difference.

Stanley (1985) misunderstood the significance of sibling species, noting that even if sibling species cannot be told apart in the fossil record, their lack of strong temporal change implies species stasis. But this misses the point that sibling species arise by speciation and yet stasis persists. Rampant production of sibling species is continually being recognized in more and more taxa, once nonmorphological criteria are explored (e.g., allozymes, DNA sequences). Stanley and his allies have failed to recognize that speciation in nearly all cases usually fails to cause morphological change. Times of extensive directional evolution are blind to the number of speciation events, even if speciation may be a consequence of local adaptive divergence. This is an important distinction, as it means that speciation is an effect, not a cause, of morphological evolution.

Are New Species Accidents or Adaptations?

We return to the difference between Dobzhansky, who thought newly derived species were exquisite adaptations, and Muller, who thought they were accidents of divergence. The adaptive aspect of species has three potential components:

1. The species is adapted to its environment, and differentially so, from other species. The process of adaptation is primarily responsible for speciation.
2. The species has a set of adaptations for avoiding hybridization with other species. These were acquired as a result of secondary contact and selection against crossbreeding.
3. The species has a gene pool that is intimately coadapted and uniquely different from other species.

This last factor could be ambiguous in that coadaptation within the gene pool might follow speciation. One can easily see why the dispute exists, given the data presented above. There is enough diversity of genetic and ecological contexts of speciation to allow strong arguments for both points of view. Indeed, Mayr's (1963) theory of genetic revolutions is somewhat intermediate. Though strong selection is important in his hypothetical revolutions, the exact trajectory of genetical properties of the new species is unpredictable.

There are some cases in which species are recognizable as ecological adaptations. This would be expected in the ecological speciation model but would also be expected with a sympatric model leading to association with coexisting species such as different host plants. The fig wasps (Agaonidae) may be an example of adaptively associated speciation (Ramirez 1970). The wasps reach maturity in a male phase. Copulation takes place before the females escape from the galls inside the fig. After copulation, the females emerge from the galls and go to the anthers, which ripen synchronously with the softening of the fig and the emergence of the wasps. The female agaonids, carrying pollen, enter the young receptacles at the time the female-phase flowers are ready for pollination. Those pollinated flowers that receive eggs become gall flowers, each nourishing a single wasp larva.

There are several hundred species of fig wasps. With a couple of exceptions, each species of New World fig (about 40 total) has its own separate wasp pollinator species. The same holds for the Old World figs. This can be proven by the inability of species of figs introduced into new areas to set viable seeds when their symbiont wasp species is absent. The one fig–one wasp relationship must have involved divergent evolution occurring intimately with the speciation process. Adaptations include the conformation of the ostiole and size of styles in figs, the morphology of mandibles and mandibular appendages, and the size of the ovipositor of wasps.

It is unlikely that the case of the fig wasps is typical. The examples of isolation correlated with chromosomal differentiation and genic sterility cited above cannot be associated with adaptive divergence. They seem to involve episodes of coincidental natural selection and genetic drift and subsequent incompatibility among geographically structured populations. The preponderance of evidence demonstrates that postmating sterility barriers are attributable to the effects of many loci (see Barton and Charlesworth 1984). It is unlikely that this aggregate cause of sterility can be related to any coadaptive interaction among the contributing genes. Here, we are looking merely at accidents of divergence. The peripheral neospecies of annual plants also seem to fall in the accidental category. Lewis's classic study (1973) of *Clarkia* demonstrated the presence of a peripherally derived "species," differing only in the shape of the petal. The parent species is superior competitively even in the sites occupied by the new species. Although the lack of superiority of the new species does not bode well for its future, the process of speciation has occurred nevertheless and seems independent of adaptive divergence. A similar case can be made for a newly derived, reproductively isolated population derived from the composite *Stephanomeria exigua* in sagebrush deserts of eastern Oregon. Individuals lack adaptations for freezing, germinate in the fall, and die in the winter (Gottlieb 1976). In this case, speciation does not reorganize the genome, but a few changes are fixed, probably by genetic drift, that are maladaptive.

Localized adaptation may enhance interpopulation incompatibility. Adaptation to temperature in a latitudinal gradient might produce local populations that suffer strongly in fitness when individuals disperse into the "wrong" latitude. This might enhance interpopulation incompatibility, as other genetic differences build up during the physiologically enforced isolation (Levinton and Lassen 1978; Lonsdale and Levinton 1985a, 1985b). The interaction between adaptation and accidental fixations, therefore, might often make it difficult to choose unambiguously between the Muller and Dobzhansky points of view.

The punctuated equilibria model and speciation. The punctuated equilibrium model purports to be an alternative to more traditional models of evolutionary change. Hopefully, the discussion presented above establishes just how difficult it is to present an "alternative" to the current diversity of theories and characterizations of evolution! The model (Eldredge and Gould 1972) established a dichotomy between phyletic gradualism and punctuated equilibrium as follows:

1. *Phyletic gradualism:* Most evolutionary change arises by gradual transformation of entire species populations. The process is mediated by natural selection and is even and slow. Morphological evolution is thus a product of gradual change within populations.
2. *Punctuated equilibrium:* Speciation is the time when most evolutionary change occurs. During the rest of a species' history, change is minimal or at least without a trend. Speciation, of necessity, is the main cause of morphological evolution. Though speciation may not involve morphological change, the punctuated equilibrium hypothesis implies that speciation at least sets the tempo of morphological evolution.

The idea of a relationship of sudden evolutionary change to patterns in the fossil record is not terribly new. It was a major theme of Simpson's Tempo and Mode in Evolution (1944). Simpson noted that sudden change was common in the fossil record and he termed such changes quantum evolution. As I will argue in chapter 6, Eldredge and Gould misrepresented the paleontological point of view, which has been always highly biased in favor of saltatory evolution, not slow and continuous gradual change. Mayr (1954) recognized this paleontological mind-set and immediately saw his model of peripheral isolates and genetic revolutions as a solution to the paleontological paradox posed by Simpson. In a section entitled "Peripheral Populations and Macroevolution" he notes that "it seems to me that many puzzling phenomena, particularly those that concern paleontologists, are elucidated by a consideration of these populations. This concerns primarily the phenomena of unequal (and particularly very rapid) evolution, rates, breaks in evolutionary sequences and apparent saltations, and finally the origin of new "types." Combined with Mayr's assertion that species are constant throughout the central parts of their range, it is clear that he conceived of punctuated equilibrium long before Eldredge and Gould. More interesting was his better understanding of paleontological practice and concerns.

Do selection models predict constant evolutionary rates? Proponents of the punctuated equilibrium theory (Eldredge and Gould 1972; Stanley 1979) have characterized neo-Darwinian selection models as predicting rates of phenotypic evolution to be slow and constant. Although it may be self-evident to population geneticists that this is far from the case, a few points can clarify this major misconception. Indeed, the only model that predicts such slow and constant change is the neutral theory of molecular evolution (Kimura 1983).

Phenotypic shifts, when they occur, are liable to be rapid and of short duration, relative to longer-term periods of stabilizing selection. Mimicry, for example, should involve stabilizing selection as long as the model–mimic system remains intact. If a new model is introduced and becomes much more frequent than the previous one, a bout of intense directional selection will cause a rapid shift, assuming that available genetic variation permits the natural selective shift. Climatic shifts are often equally sudden and will select for rapid evolutionary change. The rapid phenotypic shift in the Darwin's finch *Geospiza fortis,* following a change in climate and seed size availability (Grant 1985), is a good example.

Both mechanisms of genetic determination of character state and some selection models suggest that rectangular (constancy, sudden change, then constancy) morphological evolution is to be expected. When traits are discrete but determined by threshold effects, change may appear sudden but may be underlain by a large number of genes with an elaborate aggregate control over the discrete states of the phenotype. Thus, sudden changes of traits such as presence or absence of new ossification patterns (Alberch 1983) or the appearance of new ornamentation (Reyment 1982a) may be the result of rather simple genetic mechanisms (Levinton 1983).

Several standard population genetic models predict rectangular evolution of traits with standard population genetic parameters (e.g., Kirkpatrick 1982a; Petry 1982). If a trait is under polygenic control, and if there is environmental/developmental variance to the trait, sudden phenotypic shifts are to be expected if an environmental change involves (1) an increase in the relative height of an adaptive fitness peak, (2) a decrease in the depth of a valley between two fitness peaks, or (3) a shift in position of two adaptive peaks, bringing them close together. A shift may also occur when an increase in overall mutational input to the phenotypic variance occurs, or there is an increase in environmental–developmental variance in the character. Either of these two changes may cause a chance movement of phenotypes toward another adaptive peak. A sudden shift in the location of a single peak could also cause rectangular evolution. This overall selection scheme seems plausible and would invariably predict rectangular evolution.

Let us look at one simple example of the Wrightian adaptive landscape to demonstrate how neo-Darwinian theory is consistent with rectangular phyletic evolution.

Consider that instance where a landscape has two adaptive peaks. If the mean population phenotype is located at one peak, nearly all random deviations will be insufficient to move it to an adjacent valley. But a rare random shift of this magnitude would result in an extremely rapid move (Figure 3.16), either back to the original adaptive peak or toward the second peak (Newman, Cohen, and Kipnis 1985). Indeed, gradual change would only occur if the landscape itself changes and if peaks shift gradually and unidirectionally. When the two peaks are static, and when the mean phenotype is near one peak, the expected time until a random shift between phenotypic adaptive peaks increases approximately exponentially with effective population size. By contrast, the expected duration of transition between the peaks is insensitive to effective population size, and the transition time between peaks is likely to be much too short to be detected by the level of resolution available in the geological record (Lande 1985). This would be true for either phyletic evolution or rapid phyletic evolution following or coinciding with a speciation event.

Thus, there is no reason to believe that alternating periods of stasis and sudden change represent anything more than the standard expectations of typical selection models. There is nothing compelling about this pattern that points toward the punctuated equilibrium hypothesis that speciation is the driving force of morphological evolution.

A difficulty with the punctuated equilibrium hypothesis is its generation of the false premise that phyletic gradualism emerges as a natural property of models proposed during the Modern Synthesis (Levinton and Simon 1980; Stebbins and Ayala 1981). As mentioned above, the expectation of models of natural selection is for varying rates of evolutionary change, or usually short periods of directional change, interspersed with longer periods of stabilizing selection. Once the dichotomy is no longer valid, the punctuated equilibrium theory appears to be a solution in search of a problem.

Although I doubt that workers thought in terms of the stasis–gradualism dichotomy, even a casual inspection of the principal works of the Modern Synthesis would fall on the side of stasis. The heart and soul of Mayr's (1963) classic work is the integrity of the species. This theme reverberates in Dobzhansky's (1937) seminal volume, which viewed species as stable adaptations.

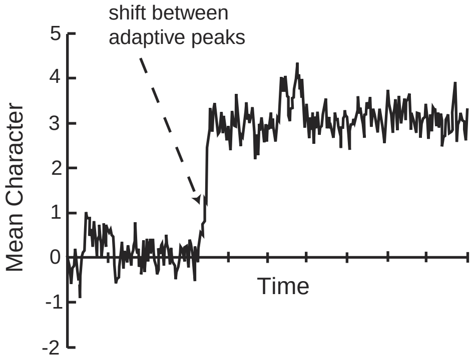


Figure 3.16. Random phenotypic evolution and the pattern of predicted evolutionary change between adaptive peaks. (After Newman et al. 1985.)

Many proponents of punctuated equilibrium (e.g., Gould 1985; Williamson 1981) have argued that stasis is a fundamental paradox, which the Modern Synthesis avoided and the punctuated equilibrium theory can solve. If species are inherently stable, then stasis is expectable. But there is no compelling reason to expect anything other than stasis, given the probable ubiquity of stabilizing selection, the evolution of stable "do-all" phenotypes in unstable environments (Sheldon 1996), and the probable rarity of the combination of novel environments and mutations required for new adaptations. Stabilizing selection has to be viewed as a more complicated process than mere culling of extreme phenotypes. Certainly one expects stasis in mimetic butterflies, so long as the model does not disappear. One is strikingly impressed with the ubiquity of additive genetic variation for morphological traits. Speciation nevertheless rarely changes them. Although some genetic changes may have correlated negative fitness effects on other traits, one can hardly imagine this to be universally so. Again, stabilizing selection is probably important in stasis that transcends the speciation process. An important part of stabilizing selection involves a sort of evolutionary paralysis caused by strong habitat selection and continuous presence of similar competitors and predators. Canalization of traits as part of a developmental homeostatic mechanism may promote constancy. But, as mentioned above, there is no strong evidence that this promoter of constancy, or its breakdown, is linked to speciation.

The evidence cited above suggests that even a restricted punctuated equilibrium model relating speciation to phenotypic evolution is similarly unfounded. Speciation may or may not involve concomitant morphological change, depending on the nature of the environments of the daughter species and the existence of variability. It is likely that phenotypic divergence in different environments would result in phenotypic divergence soon after isolation. Thus, in a restricted sense, the punctuated equilibrium claim of stasis throughout most of a species' history could be correct. But this is no vindication of the punctuated equilibrium model, which views speciation as the prime factor.

The ease with which it is possible to extrapolate within-population variability to between-species differences, as discussed in detail above, is the best evidence that the speciation process is not a major breakpoint in the evolutionary process. No set of data points to speciation as having such a role. This effectively contradicts perhaps the most important implicit prediction of the punctuative hypothesis: that within-species variation is not the stuff of between-species variation.

The Species Selection Model

Components of species selection. *Species selection* (Stanley 1975) involves selection among species whose long-term result may be a morphological trend in the fossil record. Speciation events generate among-species morphological variation, whereas selective mortality, or differential speciation rates, would bias survival in one morphological direction (Eldredge and Gould 1972; Stanley 1975). For a hierarchical theory of macroevolution to matter, one must demonstrate the importance of species-level characters in morphological trends.

The explanatory power of species selection depends on the comparative rates of response of within-species evolution and speciation rate (Slatkin 1981; Rice 1995). If genetic variability for traits is high and if mutation can fuel the variation sufficiently, then within-species evolution would be too potent a process to be outstripped by changes in the relative abundance of species with fixed species traits (e.g., a fixed allele frequency). On the other hand, species-level traits have an interesting feature. Within panmictic populations, genes are always intermixed, ever subjected to recombination and creation of new gene interactions. When a new species arises, it is the equivalent of an asexual bud (Figure 3.17). If two buds are quite different (e.g., dividing a species with clinal variation into two), their respective "traits" would constitute the variability among species. If speciation is rapid, or selective extinction is rapid, then among-species processes would matter greatly. But if the supply of variability by mutation is sufficient, then anagenic evolution would dominate within each species. As mentioned in chapter 1, extinction of an allele that dominates a species in a geographically circumscribed area can occur by means of intrapopulation selection throughout its biogeographic range, but it also can occur by broad-scale elimination of the habitat in which the allele dominates. This is the borderline between species selection and within-species selection.

A process at the hierarchical level of species could be analyzed from the point of view of natural selection, in the same terms as might be done at the individual level.

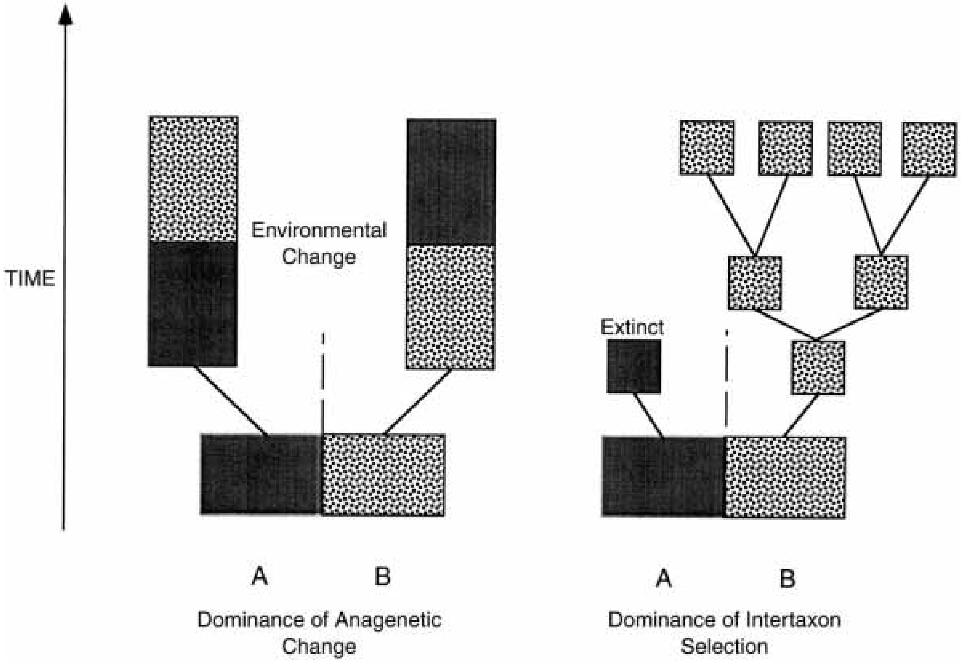


Figure 3.17. Consequences of a case in which anagenetic change dominates in comparison to speciation and extinction. On the left, phenotypes A and B comprise two parts of the geographic range of a species. Geographic isolation (dashed line) and subsequent natural selection control the phenotypes of the daughter species. On the right, the distribution of phenotypes is controlled also by extinction. (Courtesy of Sean Rice.)

We presume a source of heritable variability, a reproductive mechanism, and differential "fitness" among units – in this case, species. Differential fitness would include differential rates of speciation of different species-morphological types or differential extinction. Evolutionary trends cannot occur unless morphological variability is accumulated in speciation events, or in phyletic evolution between successive speciations. If the latter is sufficiently common, then the punctuated equilibrium hypothesis is *not* necessary for a species selection-based mechanism for directional morphological trends. In other words, we do not need to accept the punctuated equilibrium hypothesis to accept the notion of higher-level processes. Phyletic evolution and differential speciation rates could work in the same direction to produce an overall trend in a clade (Sober 1984b). This should be emphasized, given our conclusion that speciation usually does not beget morphological change. Times of intense directional change are times when intrapopulation phyletic evolution is extensive and coincident with speciation owing to locally different selection pressures, as in ecological speciation.

We must distinguish between species drift, species selection, and species hitchhiking (Levinton et al. 1986). In *species drift,* morphological trends are generated because of speciation and extinction processes that are random with respect to within-population processes. *Species selection* involves cases in which species-level properties bias speciation or extinction rates (e.g., reduced dispersal) are fixed and tend to increase the probability of speciation. This would be in contrast to the case in which organismal performance results in an increase of survival of the entire species. The sum of species selection, species drift, and success stemming from individual organismal performance amounts to *sorting* (Vrba and Gould 1986). Finally, *species hitchhiking* is the process where a given trait is proliferated in a clade, owing to its accidental association with a rapidly speciating group or with a clade having relatively low extinction rates, yet it has no particular influence on species survival or extinction. Hitchhiking is analogous to genes that change in frequency owing to their close linkage with other genes on which selection or drift is acting (Maynard Smith and Haigh 1974). For example, a morph fixed in a clade of mimetic butterflies might be common because of the high speciation rate of the clade, and not because of the adaptive superiority or any fitness characteristic of the color pattern itself. By contrast, certain traits (e.g., reproductive structures) may enhance speciation or extinction, and thus spread or diminish in frequency. This has been termed the *effect hypothesis* (Vrba 1980).

As Maynard Smith (1983) noted, the hypothesis of species selection is usually employed to cover several quite distinct claims, which are freely conflated with the punctuated equilibrium theory. *Species selection* can mean any one of the following:

1. *Tempo hypothesis:* Speciation is envisioned as the source of significant evolutionary change; evolution within the normal history of a species (i.e., phyletic evolution) is of insufficient magnitude to explain the scope of evolution (Eldredge and Gould 1972).
2. *Inherent properties hypothesis:* Selection acts on emergent properties, such as innate capacity to speciate rapidly (Vrba 1983). If points 1 and 2 apply to a given clade, then rapid evolution is ensured. Here, too, the speciation rate or measure of productivity is at issue.

3. *Competitive/adaptive superiority:* Some trait possessed by species of one clade confers competitive superiority over others or reduces their extinction rate relative to others. As a result, the group outsurvives the other clades (Stanley and Newman 1980).
4. *Radiations based on keystone innovations:* The acquisition of a keystone innovation permits a clade to diversify throughout a series of novel habitats. The increase in taxon richness ensures its survival, relative to a sister group that fails to acquire the innovation (Lauder 1981; Liem 1973).

The first two of these points fall under the punctuated equilibrium hypothesis. Both assume that speciation is important in evolution and that speciation tends to generate the sort of evolutionary change that "ordinary" phyletic evolution cannot. Point 1 certainly follows from Stanley's claim (e.g., 1979) that phyletic evolution is too sluggish to have generated the diversity of life. Point 2 depends on point 1 and implies that those groups in which speciation is inherently rapid are bound to evolve more rapidly, as they have experienced more novelty-generating speciation events. If more rapidly speciating groups are more likely to spread, then selection occurs for morphological change at a hierarchical level higher than that of individual selection.

Both Vrba (1983) and Sober (1984b) pointed out that the tempo and inherent properties hypotheses do not require the punctuated equilibrium hypothesis. Evolution can be continuous throughout the history of the species, but species-level properties might still determine the pattern of gain and loss of certain traits and species groups. Points 3 and 4, however, do not follow uniquely from a species-level process. It does not require new theory to believe that some groups will survive others as a result of their superior adaptations or competitive ability. But such survival does not indicate that the origin of the superior novelties stems mainly from extinction or speciation in the first place.

At present, it is difficult to ascribe any known trends to species-level processes. Gilinsky (1981), for example, referred to the long-term decrease in the spectrum of gastropod form through geological time as *stabilizing species selection.* Overall morph variability may have declined over time, but there is no evidence that reduced speciation of extreme morphs or accelerated speciation of common forms has been a driving force. Similarly, Stanley and Newman (1980) saw the ascendancy of the balanomorph barnacles over the chthamalid barnacles as an example of species selection, but this says nothing about the origin of the novelties characterizing the two clades in the first place – only about their current relative abundance. This example accentuates the difference in process among hierarchical levels. Within-population forces were probably important in the assembly of the two body plans. The relative extinction/speciation rates, however, might have been a case of species-level sorting (Sober 1984b; Vrba and Gould 1986), where losers disappear as taxa, perhaps by virtue of individual inferiority. This is not species selection, at least in terms of the tempo and inherent properties hypotheses. Every balanoid organism would be expected to be superior to every chthamalid organism. Thus, individual performance can be extrapolated to group-level relative survival. In any event, Dungan (1985) refuted Stanley and Newman's hypothesis for the competitive superiority of balanoids (their supposed higher growth rate due to their low-density skeleton).

Wright about macroevolution? not really. The fate of separated species in a clade can be likened to the survival of demes in Wright's shifting balance theory of evolution. Gould and Eldredge (1977) called this Wright's Rule. They argued for the random generation of morphologically divergent species – that is, random with respect to a trend. Sorting might create the trend. A series of related species might arise with a set of morphological features acquired through local adaptation. Owing to stochastic forces, one species might be more successful and spread at the expense of the others. This successful species might give rise to a new species flock and the process might then again be repeated. Through this complex web of speciation and extinction, an overall evolutionary trend might transcend the history of any one species. This process is what I mean by species drift, as defined above. Characters associated with the successful species would be proliferated and an evolutionary trend would be generated by a process above the species level. One should remember that all of this can be explained with either punctuated equilibrium or standard phyletic evolution within the history of a species.

Sewall Wright's shifting balance theory (Wright 1932; see also Provine 1986) has been mapped by Gould and Eldredge to the punctuational process of speciation and the random nature of species survival. It is worth a bit of discussion to explore whether their notion of species selection can be related readily to Wright's ideas.

The shifting balance theory is based on a set of structured demes, whose location corresponds to local maxima of fitness for given combinations of allele frequencies of many loci. With epistasis, certain allele combinations have heightened fitness over others. Selection causes climbing of these local peaks, but only at first to the nearest peak, even if it is not the highest of the entire landscape. Subsequent to this, the theory has three phases (Coyne, Barton, and Turelli 1997):

- *Phase I:* Genetic drift moves individuals in several directions along valleys between adaptive peaks, resulting in shifts toward adaptive peaks of higher amplitude. Epistatic interactions might in effect raise the elevation of the valleys and facilitate a shift from one peak to another.
- *Phase II:* Intrapopulation selection causes the invading genotypes to be selected toward the top of the new adaptive peak.
- *Phase III:* Populations occupying higher peaks reproduce more and come to dominate the adaptive landscape, which eventually consists of one fittest genotype. Higher reproduction of those at the highest peak results in more dispersal to groups at lower peaks, causing the peaks to merge to that of the highest peak.

Wright's shifting balance theory can be contrasted with mass selection, which works on a large panmictic population (Fisher 1958). As long as the reciprocal of the selection coefficient is larger than population size, the selected gene moves to fixation. By contrast, shifting balance involves structured demes, drift, differing epistatic relationships among genes at different peaks, and dispersal related to the amplitude of an adaptive peak. Wright argued that the structuring hastened selection, because random effects would actually aid in evolution of adaptation. Without the "aid" of drift, a population might be stuck in a local adaptive peak, far lower in amplitude than the highest possible peak.

Coyne et al. (1997) considered the success of the shifting balance theory and argued for the plausibility of phases I and II. Genetic drift, however, is not necessary for peak shifts. Fisher argued that complex fitness surfaces based on many dimensions would facilitate the movement of the population toward a maximum peak. Phase III is another thing altogether. If there was true population isolation, it would be extremely difficult to spread genes fixed by random populations from one population to another. But if there was spatial contact between subpopulations from the two different adaptive peaks, then the individuals from the higher peak would spread, much as an allele conferring higher fitness would spread in a cline. It would be interesting to repeat Wade and Goodnight's (1991) experiment on flour beetles, which simulated a Wrightian phase III to examine success of certain demes when introduced into others. Would normal mass selection work as well?

Also, Coyne et al. pointed out that shifting balance is unlikely to be a suitable means of fashioning a complex adaptation, supported by many genes. Indeed, this is the fundamental flaw of punctuated equilibrium as a creative force in evolution. All of the traits that matter could not be fixed by any process that we now understand. It is therefore not likely that a series of morphologies would be generated as species in a Wrightian framework.

The shifting balance theory is an elegant explanation for population subdivision, the development of multiple adaptive peaks of differing amplitudes, and the possible spread of "good genes" from one adaptive peak to another. Ultimately (and ironically), it is not a justification for punctuated equilibrium, because the most adapted genotype ultimately wins in Wright's scheme (Wright 1932). Scaling up to the species level, Gould and Eldredge made an inappropriate analogy to argue that species (analogous to demes) appear randomly and one might survive, perhaps randomly. But Wright's model incorporates demes at local adaptive peaks. This is far from a random model. Indeed, it is formally possible that all such demes will consist of a similar phenotype, with slight variations in fitness. It is therefore peculiar that Gould and Eldredge used Wright's theory, even as a metaphor for nonadaptive speciational generation of diversity.

The supposed contest between Wright and Fisher loses much force when one considers that we know so little about the aspects of population structuring that would matter in natural selection and speciation. Do large populations fail to have sufficient variability to evolve? This seems unlikely. Most traits examined have strong narrow-sense heritability, suggesting the maintenance of genetic variation even in large populations. Further, there seems to be sufficient variability generated by mutation to allow for further evolutionary response in large populations (Lynch and Lande 1993). Finally, selection in nature is typically strong, which would suggest the rapid spread of favored genotypes pretty much as the Fisherian model would require (Endler 1986).

Traits hitchhiking phylogenies. Extinction events tied to major habitat alterations may be the best potential example of hitchhiking, where a trait disappears, but not because of its decrease of individual fitness. If a clade arises with a given fixed trait, and if that clade is restricted geographically, then a regional climatic change (e.g., a local marine regression) might eliminate the clade. Fürsich and Jablonski (1984) described a clade of boring gastropods that arose in the Mesozoic but ultimately did not survive. It would seem unlikely that the extinction of this clade was due to the presence or absence of the ability to bore into hard skeletons, given the likely continual abundance of skeletonized prey. On a larger scale, mass extinctions probably have eliminated many groups, not because of their species-level properties but because of their bad luck in being in the wrong place at the wrong time. On the other hand, some marine groups may have survived mass extinctions as a result of their relative insensitivity to pronounced changes in primary production (e.g., Levinton 1974, 1996).

As opposed to species drift, species selection requires a species-level property that confers relative survival or increased speciation. At the hierarchical level of species, this is the equivalent of a relatively fit genotype. Dispersal type might strongly influence species-level origins or extinctions (Jablonski 1979). In marine invertebrates, reduced dispersal seems correlated with rapid speciation and extinction (Hansen 1980; Spiller 1977). This precarious balance might shift in different cases, favoring one clade over another. If a favored clade had species with some fixed trait (e.g., pronounced ornamentation), then the trait would become more common by species hitchhiking.

Eldredge and Gould (1972) suggested that speciation might generate a set of new morphotypes that are randomly arrayed, but species selection would cull out a biased fraction, thus producing an evolutionary trend. It seems absurd to expect the random generation of variant species suggested by such an undirected speciation hypothesis. A variety of functional, genetic, and developmental constraints will restrict descendant morphologies to a reduced range of morphological possibilities (Levinton and Simon 1980; Maderson et al. 1982; Muller 1949). Stanley (1979) suggested that directed speciation would produce a biased array of descendant morphologies. The concept of directed speciation is only as strong as the concept that speciation is the primary generator of morphological change in the first place. Directed speciation does little more than claim that speciation accelerates a phyletic trend. In the worst case, a single string of ancestor–descendant morphologies, unbroken by any cladogenesis, would be thought to be a series of speciation events (see chapter 6). The model here would depend on relating speciation to morphological change, which in the case of fossil lineages would result in a tautologous relationship between the two (Levinton and Simon 1980). In many fossil cases, directed speciation amounts to uneven rates of phyletic evolution (Levinton 1983; see chapter 6).

It might be argued that gene mutation is no less subject to biased change. Therefore, gene-level mutation is completely analogous to Wright's rule. This might be true, with the important exception that surviving species probably consist of individuals that are in some sense functionally harmonious with their environment. Newly arising species, subject to strong direction selection, may evolve only a limited set of morphologies. This is in contrast to genic-level morphs that assort within populations. Those with low fitness will eventually disappear but will most likely appear no less randomly than those with increased fitness. In contrast, species are not likely to have this random aspect. The analogy between gene mutation and species level divergence holds only when all possible daughter species morphologies are functionally viable. I contend that this is uncommon.

Given the undirected model of speciation, and success of a small fraction of a clade, can we distinguish between the punctuated equilibrium theory and phyletic gradualism possibilities? Slatkin (1981) used a diffusion model of evolution to assess the possible relative contributions of speciation and phyletic evolution in an evolutionary trend. In a random model, the relative importance of speciation and phyletic evolution in creating among-species variance in morphology depends on (1) the within-species phenotypic variance, generated by unpredictable changes in phyletic evolution due to either genetic drift or randomly fluctuating selection forces, and (2) the variance of phenotypic change per speciation event, generated by random changes in phenotype occurring at speciation.

For speciation to be the principal cause of between-species differences in a clade, the product of the speciation (per generation) rate, *s,* and *Vs* would have to be greater than *Vp,* which is the product of heritability, effective population size, and the variance in the character. For mammals, *s* is estimated to be 0.4 per million years. If heritability is 0.5, with a generation time of 2 years and an effective population size of 1,000, the contributions of speciation and phyletic evolution would be equal if the morphological variance generated by speciation were 625 times the phenotypic variance (Slatkin 1981). For a completely neutral character, the standard deviation of the change in the average value during speciation would have to be 25 times the within-species standard deviation for the speciational and phyletic components to be equal. This does not bode well for the species selection or drift processes as a generator of morphological trends, because such cases are likely to be rather rare. One would require a combination of low heritability with high effective population size to change this conclusion substantially. With the undirected speciation model, any instance of directional selection will inevitably cause the phyletic component to be yet more important than the speciational component, as a directional change will occur at every generation in phyletic evolution, but not at speciation events.

In some cases, speciation might play an important role in morphological trends. For species selection to work, the life span of a species must be short relative to the mutation rate. Using a model that combined intraspecies and interspecies selection, Rice (1995) demonstrated that there may be examples of species life spans that are short enough relative to a mutation rate of 10:6. But morphological mutation rates are typically far higher, as high as 10:2, owing in the main to the control of many genes on traits (Lande 1983). Therefore, realistic measures militate against the power of species selection to vanquish the force of intraspecific population processes.

These arguments suggest that it is extremely unlikely that complex structures, or even genetically simple structures, ever arose by species drift. The potential for phyletic evolution is immense and is certainly far more potent than a mechanism that effectively depends on a process analogous to neutral evolution. Selection is always more powerful than drift in producing trends. Given that speciation generates less variance than phyletic evolution (Slatkin 1981), this should apply even when we are comparing selection within populations to drift among species. Even in the case of species selection, Slatkin's arguments tip in favor of the power of phyletic evolution.

Even without this argument, it is inconceivable how selection among species can produce the evolution of complex morphological structures. The elaboration of some of these structures has of course taken more than the life of any one species; cladogenesis is coincidental to any major evolutionary trend, but it does not follow that it is a causal mechanism. If anything, cladogenesis may slow down the evolution of complex structures, simply because species are continually winding up in new and complex environments that might constrain the further improvement of a structure down a main evolutionary path. In contrast to the arguments of Stanley (1979), phyletic evolution is the likely source of complex adaptations, whereas species drift or selection is likely to bring about evolutionary trends such as changes in overall body size or degrees of ornamentation. Species selection did not form an eye or a secondary palate.

The ecological component of speciation is perhaps the most compelling argument against the notion that species are just produced willy-nilly in any direction, with no regard to natural selection. This is the most fundamental claim of punctuativists in attempting to connect punctuated equilibrium with selection at the species level. This argument is simply preposterous, as it ignores the environmental context of many speciation events, which isolates populations that are spread over broad environmental gradients and often produces ecological isolation on a much more microscopic scale, where local subhabitats select for habitat affiliation and result in preferential mating (Feder et al. 1990a, 1990b; Rundle et al. 2000).

If morphological change per speciation event showed no temporal trend through the history of a clade, then morphological evolution should accelerate with time. The number of speciation events per unit of time should increase as the clade becomes speciose. Species richness usually increases during the early history of a clade. But it is well known that the rate of morphological evolution usually decelerates with time. This is best recorded by the ratio of taxonomic species to families, which tends to increase with geologic time (e.g., Valentine 1969). The decoupling of morphological diversity from speciation rate is registered clearly in Foote's (1991) analysis of taxonomic and morphological diversity of blastoids. Generic richness peaked in the Lower Carboniferous, but peak morphological diversity is found in the Permian. Generic richness rose from the Ordovician to the Lower Carboniferous then dropped off, but morphological diversity increased nearly until the group's demise. Relative to taxonomic richness, blastozoan morphological diversity peaked in the Cambrian. A small number of Cambrian taxa sparsely occupied an expanse of morphological space, but subsequent diversification involved expansion and filling of morphospace (Foote 1992). Given the correlation of systematic rank with phenetic diversity, these trends suggest a decelerating rate of generation of morphological diversity, even if it is steadily increasing in some cases, perhaps toward a plateau. Most morphological novelties appear early in the history of a clade, and directional change tends to decelerate over time (Cisne 1975; Westoll 1949). These considerations strongly weaken the model of species selection, as it relates to accumulating change with speciation events. Some other process would have to be invoked that explains why morphological change per speciation event has declined with time.

Although speciation is not likely the typical source of adaptive evolution, the peripheral nature of new species (Mayr 1963) often places them in ecologically marginal environments. These marginal environments have a much lower probability of survival than the larger parental species and the newly budded species would be expected to disappear. This can be seen in the broad-ranging species of marine invertebrates that occasionally give rise to peripheral species. The mussel *Mytilus edulis* most probably gave rise to the Mediterranean *Mytilus galloprovincialis*. It seems unlikely that the latter will survive, so long as its future is tied to so unstable a peripheral basin (which it is not, owing to human introductions elsewhere). Similarly, the eastern North American bivalve *Mulinia lateralis* gave rise to the morphologically divergent *Mulinia* pontchartrainensis. The latter is restricted to a geologically unstable lake, and will likely go extinct. These two cases suggest that peripheral species may be morphologically divergent but will not stand the test of time. The survivors will be the large widespread species that are liable to remain morphologically static. This expectation is realized in the data of Stanley and Yang (1987), who found extensive constancy in many Atlantic coast bivalve mollusk species over many years.

In conclusion, there is little evidence to support the notion that speciation is an accelerator of evolution or even an arbiter of directional morphological trends; the potency of phyletic evolution suggests its likely primacy in the evolution of functionally integrated forms. It does not follow, however, that the present relative abundance of taxa with different morphological character complexes relates strictly to phyletic evolution. Relative extinction and origination may explain current distributions. Although relative extinction may be related to superior adaptedness conferred by given characters, it is also possible that success may relate to a given group's sheer number of species. During a crisis, a severe climatic change might favor the group that produces the most species and spreads them over the most habitats. In this important sense, species drift and species selection may have explanatory power in the quest to understand dominance patterns among taxa.

The Main Points

1. The process of speciation is incompletely understood because it occurs on a timescale that is inaccessible to biologists and paleontologists. Most of our information comes from static descriptions of genetic and phenotypic variation within and between species.
2. Variability in chromosomes, allozymes, and morphology has been examined extensively in natural populations and species. The bulk of the evidence suggests that the sort of variation found within species is qualitatively similar to that found between closely related species. In the case of allozymes, there is a smooth increase in degree of differentiation from intrapopulation, to closely related interspecific, to more distantly related interspecific comparisons.
3. Although reproductive isolation is the natural criterion for recognition of different species, it is not always clear how the speciation event took place. Substitutions of alleles at single loci and fixation of chromosomal variants may both be important. Hybrid zones have often been investigated to surmise the processes that maintain isolation. Many of these, however, are probably quite ancient and species are probably long divergent. Postmating isolation is now rather well known for

Drosophila, but most premating isolation can be shown to have evolved in the presence of sympatry.

4. Speciation has been explained as an accident of geographic divergence, resulting in fixation of alleles producing sterility, or as an adaptation that serves to avoid hybridization of separated populations that have recently come into contact. Although it is clear that speciation seems associated with geographic separation of populations, divergence can occur even with modest dispersal between the populations. Most speciation events probably are due to fixation of new alleles in complete or modest isolation, resulting in sterility with the most closely related population. In some cases, it is clear that this fixation in isolation is associated with natural selection for new environments. In a few cases, the process of adaptation is the very same one that results in the formation of new species, as when a tight relationship evolves between a population and a new host. Ecologically driven speciation may result in eventual sympatry of species with fitness in complementary microhabitats.
5. Many have suggested that dramatic genetic reorganizations occur during species formation, often in peripheral and very small populations. Although this is theoretically possible, the genetics of closely related species usually fails to support such revolutions, despite cases known where bottlenecks can be shown to have occurred. Important exceptions include the polyploid origins of many plant and some animal species.
6. The punctuated equilibrium model argues that morphological change is associated with speciation and that species are static during their history due to some internal stabilizing mechanism. There is no evidence coming from living species to support this. If anything, recent research has demonstrated that speciation occurs typically with little or no morphological change; hence the large-scale occurrence of nearly identical sibling species. As Haldane pointed out (1932a), within-species variability is readily extrapolated to between-species variation.
7. Trends in morphological change might emerge from patterns of speciation and extinction. These need not be associated with punctuated equilibrium. Certain species-level properties, such as geographic range, might influence speciation or extinction rates. Alternatively, a random process (species drift) might cause speciation and extinction rates to permit some taxa to expand (or contract) relative to others. Associated morphological properties might hitchhike and expand or contract in frequency, as the result of either species selection or the species drift process. Although these processes are not likely to be the reason for the evolution of complex morphological features, they might explain the predominance of a given morphology at any one time. This might, in turn, influence the variation available for adaptation. The punctuated equilibrium model is not required for species selection, because species-level processes could work in tandem with phyletic evolution to produce trends.

CHAPTER 4

Development and Evolution

> "Fashion me, therefore, one form of a many-colored and many-headed beast. There is a ring of heads both of tame and wild beasts, and it can change and produce them out of itself at will."
>
> "That is clever molder's work," he said.
>
> – *The Republic* of Plato

Constraint and Saltation

Developmental biology has long been a focus for evolutionary theory (Bonner 1982; de Beer 1958; Garstang 1922; Goldschmidt 1938; Gould 1977; Haeckel 1866; Raff 1996; Raff and Kaufman 1983; Waddington 1940). Evolution can be seen as a change in developmental programs that elaborate the phenotype. The effects of genes and the range of genetic variation would best be investigated on a mechanistic basis, yet until the 1990s, we had only a very small window on this enormously important developmental landscape.

Once we can understand the nature of development and how it constructs the phenotype, we confront anew some of the age-old questions of evolutionary biology. Development is legendary for its organization, sometimes appearing to be remarkably automatic and even self-organizing. The strong integration of the developmental process might not easily be breached by a mutant, which would disrupt fundamental and tightly integrated cellular and molecular processes. This would suggest a force for conservatism in evolution. On the other hand, the tremendous organization of developmental processes suggest to many that simple genetic changes might beget enormous saltatory evolutionary change.

The Janus-headed coin of development is illustrated well by the evolutionary change of the tail in ascidian tadpole larva, which has been lost in evolution several times independently (Jeffery 1997). Although the adult is a sessile suspension-feeding gelatinous organism, the tailed larva has a notochord and a dorsal central nervous system, the hallmarks of a chordate. In about 20 species, the larva lacks a tail and associated brain-sensory organs (Figure 4.1). This major switch in morphology is associated with a mundane larval adaptation for reduced dispersal by the tail-less form. (Tadpole larvae are not brilliant dispersers, either.) Tail-less development

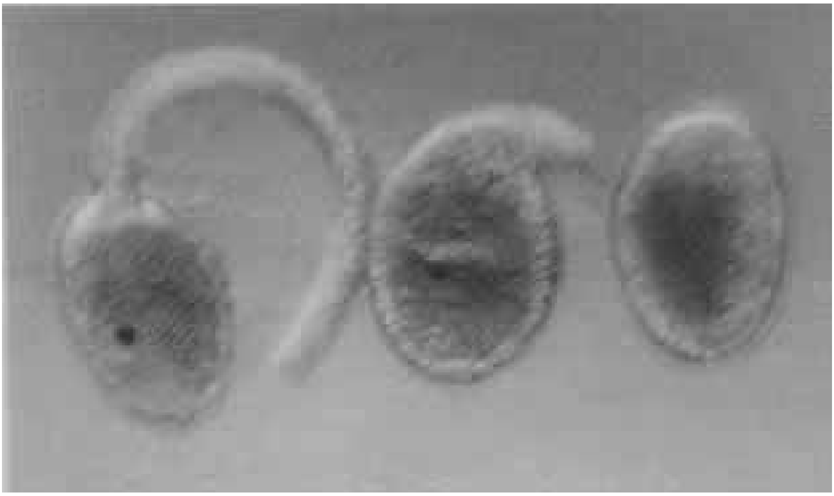


Figure 4.1. Tailed (*Molgula oculata,* left) and tail-less (*M. occulta,* right) ascidian larvae. The center larva is a hybrid, where partial tail morphology is restored. (After Swalla and Jeffery 1996, with permission from the American Association for the Advancement of Science.)

results from the abbreviation of developmental programs owing to maternal message and gene regulation in the zygote. The zinc-finger gene *Manx* is expressed in tailed species but is downregulated in tail-less species, which suggests a simple mechanism for a momentous developmental reorganization, dropping some of the lynchpins of the chordate anatomical plan (Swalla and Jeffery 1996).

The message told by the *Manx* gene is not clear, despite the elegant experimental results. On the one hand, it tells us that it is rather easy to lose the tail and a host of associated developmental trajectories (e.g., notochord, tail, otolith, and muscle cells). On the other hand, this change is present in only about 20 species of the 3,000 total species of Ascidia. The change to the tail-less condition is, moreover, confined to only two families, Molgulidae and Styelidae. If it is that easy, why is it so uncommon? Again, we face the two faces of constraint and possibility for major change.

Time and again, the concepts of constraint and saltation have been formulated in terms of development. Developmental constraints are nonrandom channelizations of evolutionary direction due to limitations imposed by complex interactions of gene expression and epigenetic interactions, such as tissue inductions, in the developing organism. The disruption of such interactions may strongly influence fitness and therefore restrict evolutionary change. In the context of development, saltations are rapid evolutionary fixations of phenotypic discontinuities guided by developmental controls, which do not permit continuity of form in polymorphic populations. It is the purpose of this chapter to discuss these two concepts critically, along with the role of development in evolutionary change.

The Holy Grail: Connecting an Understanding of Genes and Development

The founders of the neo-Darwinian movement recognized the importance of development in evolution (Ford and Huxley 1927, 1929; Haldane 1932b; Lande 1980b;

Orzack 1981). Despite this, embryology at first influenced the study of phylogeny more than the study of genetical mechanisms of evolution (de Beer 1958; Nelson 1978). Embryology parted company with genetics long ago. The influence of Haeckel's biogenetic law on embryologists suppressed the expectation of much evolutionary change in embryos (Raff and Kaufman 1983), even though today it is rather clear that at best, there are only brief stages of development that unite form among distantly related embryos (Gerhart and Kirschner 1997; Raff 1996). The alliance with Haeckel led to a schism between embryologists and the developmental biologists, who adopted a more mechanistic approach but abandoned evolutionary thinking (Gross 1985).

Even though general embryology was far removed intellectually from genetics, many developmental systems were actively studied by geneticists. Mutants in vertebrate skeletons and developmental mutants in *Drosophila* and other insects gained favor as popular experimental systems. The schism probably could have been bridged by our past century's greatest population genetics theorist. Sewell Wright's first research on toe number determination in guinea pigs could have been the pioneering launch of a more general understanding of developmental–genetic interactions (see Wright 1934a, 1934b). I expect that the difficult nature of quantitative genetic studies on traits with strongly determined (canalized) alternative states and the poor communication among fields led to the diminutive role of development in population genetics. It is also likely that development was simply too poorly known to be easily studied from a mechanistic point of view, let alone integrated with evolutionary genetics. Britten (1982) and Davidson (1976) both discussed the extent of our ignorance of the most basic aspects of gene action in early development as late as the 1980s. This could not have been encouraging to geneticists who were anxious to get "closer and closer to the genes." As it turned out, we had to wait a decade after Britten and Davidson's publications before things got much better.

We now are at the threshold of a completely new period, in which development and genetics are being connected in great detail. At first, this became apparent from the emerging understanding of ubiquitous genes that exert the same developmental control in many distantly related taxa. Most famous are the Hox-type genes, whose axial specification of form spans the phylogenetic chasm between vertebrates and arthropods.

At the time of publication of the last edition of this book (1988), there was an emerging understanding of a widespread homeobox sequence that united all of the triploblastic animals at least. Now, modern methods of gene sequencing, manipulation of gene expression, and tracing of spatial patterns of gene expression have resulted in an explosion of information that is not leading, as yet, to many useful evolutionary rules. So far, we are seeing the same errors promulgated in lionizing past laws of ontogeny and phylogeny. Beliefs in major genetic revolutions, master switch genes, and other universals are beginning to form a modern version of the ontogenetic laws of old, with little consideration for the possibilities of convergence in developmental gene function. Nevertheless, the new tools allow us a better peak through the curtains, and the early flush of enthusiasm will likely be followed by substantial advances in development and evolution.

Phylogeneticists and Developmentalists

The significance of development in evolutionary theory evolved from both phylogeneticist and developmentalist viewpoints. The phylogeneticists view ontogeny as the source of information of an organism's evolutionary history. Ernst Haeckel, that most devoted German disciple of Charles Darwin, combined a materialistic view of evolution with a belief that humankind's ancestry was recorded in the sequence of embryonic development. He rigidly associated the order of ontogeny of derived taxa with the order of acquisition of ancestral character states, which invited strong later criticism (de Beer 1958; Garstang 1922; Gould 1977; Raff 1996; Raff and Kaufman 1983). These criticisms, however, failed to erase the fact that phylogeny was recorded to a strong degree in development, even if there were strong alterations. Developmental sequence can provide phylogenetic data.

But why should development be indicative of ancestry at all? Why do ancestral structures that are degenerate or absent in the adult often make an appearance, albeit briefly, in the embryo, only to later appear as vestigial structures or even to disappear? How can we explain the occasional reappearance of ancestral structures as developmental abnormalities that supposedly disappeared millions of years before in evolution? Why, for example, do some whales have hind legs (Andrews 1921), and why does the occasional horse have toes reminiscent of their likely ancestors instead of having just splints (Marsh 1892)? Many embryos routinely express structures of ancestors, as in the embryonic teeth expressed in baleen whales. The evolutionary process does not erase an underlying developmental infrastructure.

The developmentalists claim that "the diversity of structures that have been formed through the process of evolution is constrained by the rules which govern pattern formation during development" (Stock and Bryant 1981, p. 432). As such, evolutionary change of necessity is the evolution of developmental sequences. The individual, therefore, is treated in terms of its entire ontogeny, and development is therefore both the constraint and target of selection. There is a developmental toolbox, and certain tools may be used in many contexts, but this does impose a possibly limited set of alternative developmental pathways.

The developmentalist claim should be the key to the phylogeneticist claim. If we can understand whether development really does provide constraints, and if we can understand how developmental programs are shaped by evolutionary processes, then we might come to understand the limits to which phylogeny can be expressed in ontogeny. Unfortunately, nearly all evolutionary debate in the past has centered on the reverse of this thought process. Theorists have used a belief in the fixation of embryological patterns as the phylogenetic key to explain developmental sequences in extant organisms. This approach fails to take notice of many of the advances of developmental biology in the twentieth century that point to a lability in the mechanisms of development. This lability is also beginning to become apparent in molecular data, despite the superficial appearance of conservatism.

Development: constraints and discontinuity of form. The importance of constraint and discontinuity of form in populations has been long appreciated on both genetic and morphological grounds. Wright's (1934a, 1934b, 1935a) classic analysis of digit number in guinea pigs recognized the constrained nature of development, despite complex polygenic effects on traits. Quantitative geneticists working on mutations affecting vertebrate skeletons and teeth have long been aware of the presence of limited and discrete variation (e.g., Garn, Lewis and Vicinus 1963; Green 1962; Grewal 1962; Grüneberg 1965; Hadorn 1961). Sinnott and Dunn (1935) showed that plant development is strongly regulated by genes that affect rates and by genetically controlled quantum changes in morphology (see also Haldane 1932b). Extreme fruit-shape differences are already established in the very earliest primordia of squash. Many of the strong differences among genotypes can be attributed to phenotypic changes early in the developmental process (e.g., Atchley, Riska, Kohn, Plummer, and Rutledge 1984). In plants, mutations affecting early stages of development often have the most significant final effects on overall form. Form differences are usually not the result of "mere continuations or extensions of the later stages of a growth period" (Sinnott and Dunn 1935, p. 140).

Why might there be constraints? The developmentalists emphasize the quantum nature of development. The origin of structures is not continuous but discontinuous, often determined by a cascading set of gene activations. Despite the potential continuous nature of additive gene effects and the continuous possible range of transcription regulators, morphogens, hormones, and other developmental messages, morphological structures often come as complete structures or not at all. Of equal interest is the importance of localization in development. Embryos develop only as the result of a complex series of timing events that bring different cells into contact or place cells or molecules of restricted developmental potency in a proper environment for induction. The spatial position of cell groups seems crucial in the generation of morphological patterns, owing to

- Localized intercellular movement and regional movement of dissolved substances that often set gene expression in motion (Garcia-Bellido, Rippoil, and Morata 1973; Summerbell 1981; Turing 1952; Wolpert 1969)
- Transcellular electric fields (Jaffe and Stern 1979; Nuccitelli 1983)
- Mechanochemical interactions (e.g., Odell, Oster, Alberch, and Burnside 1981; Oster, Murray, and Harris 1983)
- Specialized cell adhesion molecules (Edelman 1986)

Must these not influence the direction of evolution? These two phenomena – integrity of structure and topological restriction of development – suggest that an embryo can be transformed in only a limited number of directions during the process of development and evolution. That is the fundamental message about form that Richard Goldschmidt's pioneering book *Physiological Genetics*[1] (1938), derived from Spémann (1938), underscored so well.

Some examples of developmental mutants show the discontinuous and often spectacular nature of possible structural change. Consider the *cyclops* mutant (Bowen, Hanson, Dowling, and Poon 1966) of brine shrimp males (Figure 4.2). After the fourth instar, the lateral eyes move forward and fuse together, forming a

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[1] This book is still must reading for students of development and evolution.

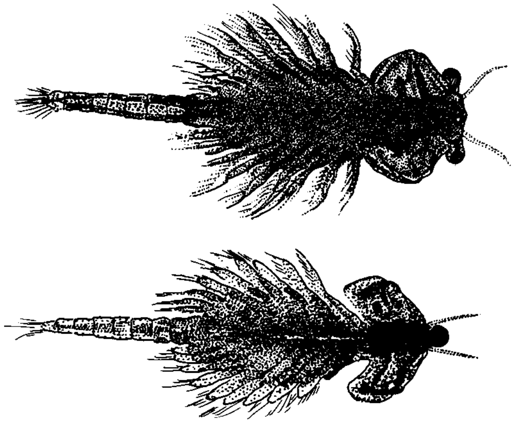


Figure 4.2. Dorsal view of normal living male brine shrimp *Artemia salina* (top) and *cyclops* male (bottom). (Drawn after Bowen et al. 1966.)

single large compound eye by the ninth instar. During this fusion, the ganglia and nerves of the two optic stalks fuse; the resultant eye resembles the normal medial eye of the cladoceran *Leptodora*. Thus, a quirk of development has caused a structure to change from that characteristic of one taxonomic order to another! The development of the vertebrate limb shows similar quantum steps. Alternative symmetries and structures, demonstrated by manipulations of development and repair, can be spectacularly different. An excision of the posterior part of the chick (*Gallus gallus*) wing bud results in the elaboration of only a single skeletal element: a humerus, or a humerus fused with a reduced radius. If, however, the anterior part of the bud is excised, the posterior half develops nearly normally, elaborating part of the humerus, the ulna, and digits 2, 3, and 4 (Hinchliffe and Gumpel-Pinot 1981). Clearly, developmental mechanisms are well organized, depend on tissue interactions, and often involve discrete steps (Alberch 1980; Maderson 1975).

A developmental notion of macromutation springs from the nature of development described above. If a simple transplant places toes on wings or replaces scales with feathers, why couldn't evolution occur in major steps? Some have seen such discontinuities in development as a vehicle for major evolutionary jumps (Goldschmidt 1940; Gould 1980a; Løvtrup 1974; Maderson et al. 1982; Schindewolf 1936, 1950), or at least see them as the possible stuff of major saltations (Alberch, Gould, Oster, and Wake 1979; Frazzetta 1970).

The Nature of Gene Activation in Development

All genes are in most cells, but gene activation is local and timed specifically. Development from the zygote is truly a remarkable process. A spatially complex organism develops from a geometrically simple fertilized egg. What is the role of the genome in such a process? We would like especially to understand the distribution of the genes and their effects. Are all genes in all cells? Are all genes activated in all cells? If not, are they turned off? Is this an irreversible process? The reader should consult Davidson (1976), Gerhart and Kirschner (1997), Gurdon (1974), and Stewart and Hunt (1982) for further information on the subject.

All genes seem to be in all cells, with some important exceptions such as vertebrate red blood cells. At the crudest level, DNA and chromosome content seem to be constant among somatic cells. This conclusion is bolstered by other studies such as DNA–DNA hybridizations and by the partial and sometimes total developmental potential of differentiated cells. In the former case, separated DNA strands from differentiated cells hybridize with DNA from early embryonic cells at the same rate as hybridization among embryonic DNA strands (McCarthy and Hoyer 1964). Because the rate of hybridization is a function both of overall DNA content and the heterogeneity of (mainly repeated DNA) sequences, hybridization rate is a crude approximation of sequence similarity.

To demonstrate cell potentiality, the nuclei of differentiated cells can be transplanted into earlier developmental milieus. If a complete organism develops, then we conclude that the complete genomic complement is present in the differentiated cell and that the genes have not lost their potential. If a complete organism fails to develop, all genes may still be present, but some may have been irreversibly switched off. (Some embryos are *mosaic* – cells have fates determined early in development that cannot be reversed by transplantation. *Regulative embryos,* in contrast, determine cell fate by the surrounding cell environment.) Such experiments have been done successfully in the clawed toad, *Xenopus laevis,* where endodermal cell nuclear transplants into anucleate eggs result in normal development to the adult (e.g., Gurdon 1974). Similar experiments have been performed successfully in mammals and *Drosophila* (Ilmensee 1976; Ilmensee and Hoppe 1981).

Despite the nucleic acid homogeneity, a spatially complex embryo develops. Spatial inhomogeneities must be present initially or generated subsequently to elaborate the embryo and the subsequent adult organism. The same can be said for timing. Temporal differences in gene action contribute to the development of the embryo by affecting the temporal distribution of gene products. In the cases of both spatial and temporal change, two sources of heterogeneity are crucial: (1) properties of the egg cytoplasm, creating a template for spatial differentiation, and (2) successive factors which cause varying spatiotemporal expression of different gene complexes.

The cytoplasmic environment is an obvious source of inhomogeneity. Egg cytoplasm contains mRNAs produced before zygote formation or gene activation in the egg nucleus. Initial dominance by mRNAs of maternal origin may eventually give way to dominance by embryonic nuclear genes, but the former may strongly influence early development in conjunction with embryonic gene action. In the 16-cell stage of the sea urchin embryo, about 90% of the mRNA present is maternal in origin. Maternal message continues to be translated in the embryo even though gene products such as tubulin are also inherited via the egg cytoplasm (Davidson, Hough-Evans, and Britten 1982). The initial micromeres may be dominated more by nuclear gene activity than other cells in the embryo, as judged by their higher than average histone-to-nonhistone ratio. The onset of amphibian gastrulation, following a switch from synchronized to asynchronous cleavage, may be regulated by the gradual increase of nuclear dominance over cytoplasmic maternal inheritance, or by a timing system (e.g., Aimar, Delarue, and Vilain 1981).

In fruit flies, the posterior pole plasm appears early in development and is the locus of formation of germ cells in the adult. This site is determined by localization of a messenger RNA of maternal origin (Mahowald 1968). Similar localization can be seen in the anuran amphibian egg, where a subequatorial location in the uncleaved egg is necessary for the development of a normal embryo (Spémann 1938). Subsequently, other fly tissue layers are determined with reference to this site (Gerhart, Black, Gimlich, and Scharf 1983). Transplantation of the region to the opposite side of the egg results in duplicate normal embryos. As development proceeds, more and more such reference points provide a series of foci for developmental instructions. These organizers (e.g. Spémann 1938; Waddington 1940) are the principal part of the localization phenomena that permit the development of the embryo's spatial complexity. The process of sperm entry creates a spatial reference point that can affect the spatial pattern of subsequent embryogenesis. The rate and time at which such reference points develop is strongly variable. In mammals, for example, reference points seem to develop later than in anurans.

The nature of organizers in early development may be constant throughout the animal kingdom. In both the nematode *Caenorhabditis elegans* and the fruit fly *Drosophila melanogaster,* the anteroposterior axis is initiated by means of repression of translation in the posterior pole. In *Drosophila,* the gene *bicoid* operates at the anterior pole, whereas *nanos* operates at the posterior pole. Mutant flies of *bicoid* often lack head and thoracic segments. Repression of another gene, *hunchback,* by *nanos* in the posterior region allows the anterior production of *hunchback* mRNAs. The anteroposterior gradient of *hunchback* action in the fruit fly sets the anteroposterior differentiation process in motion (Kimble 1994). A similar process sets off the anteroposterior axis early development in *C. elegans,* although *bicoid* itself is not found outside of higher Diptera.

Temporal change in gene action is also an important aspect of development. Batteries of genes are successively turned on, particularly in localized groups of cells. What information is needed to turn on such batteries in higher organisms is beginning to be understood. Davidson and Britten (1971) argued that following an initial inhomogeneity of egg cytoplasmic regulatory elements among the cells in early cleavage, alternative sets of genes are turned on by diffusible products of integrator genes. Activation of a given master integrator gene set could shut off the synthesis of a regulatory macromolecule, maintaining the organism in the previous state of differentiation. These regulatory events were already known in prokaryotes, and Britten and Davidson presaged an explosion of understanding in eukaryote development. Such regulation could switch on many loci by such *regulatory gene* action, which affects the expression of *structured genes* that produce proteins.

Tissue-specific changes in chromosomal morphology are well known in the polytene chromosome puffs in the embryos of *Drosophila* and in the lampbrush chromosomes (Y chromosomes of *Drosophila*) and in the chromosomes of *Xenopus.* Puffs are sites of active gene transcription and often a cloud of mRNA surrounds the chromosomal DNA. In situ hybridization experiments in dipterans show that polytenization of chromosomes during development is localized and genes produce increased numbers of transcripts. In *Drosophila melanogaster,* tissue-specific increases of amylase correlated with the degree of chromosome puffing at the locus (Doane, Abraham, Kolar, Marenson, Deibler 1975). In the past, this was the best evidence that batteries of genes are probably being turned on sequentially and suppressed during development. Temporally specialized embryonic, juvenile, and adult loci may sequentially produce different proteins serving analogous functions (as in the globins: Edgell et al. 1983). It is the localized action of specific sets of genes in spatially separated lineages of cells that partially gives development its characteristic sequential restriction of cell morphological and physiological fate.

Gene activation is initiated by threshold concentrations of a number of dissolved and diffusible substances, some actively transported across cell membranes to activate nuclear gene sets. For example, the sequential switching on and off of successive gene batteries in insects is partially under the influence of the hormone ecdysone (Ashburner 1980). If a third-instar *Drosophila* larva is cinched at the midline, the posterior region cannot receive ecdysone and juvenile chromosomal puffing patterns are maintained. The anterior portion contains the ecdysone-secreting ring gland and develops normal puffing. Ecdysone probably combines with a receptor to activate early puff regions and inhibit later puff regions. At the same time, a protein produced from genes in the early puffs eventually reaches a concentration sufficient to cancel the inhibition of ecdysone, and the late puff is activated (Ashburner 1980).

The complexity of timing of gene action. Given the activation of gene batteries by selector genes and the role of timing in gene expression, it becomes clear how simple genetic changes can greatly alter the track of development. Consider the simple developmental program of traits x and y, diagrammed in Fig. 4.3. The traits are defined as fully differentiated cells with complete function at times F_x and F_y, respectively. The cells have some expression at time E (e.g., can be identified as a pancreatic cell but not fully secretory) but have been determined at time D; their subsequent fate as a fully differentiated cell is sealed. We will ignore for now a time before D, when the cell fate is specified but can be reversed by the local cell environment. After time D_x, other developing cells can "know" the identity of cells of type x, either by direct contact or by detection of a diffusible substance.

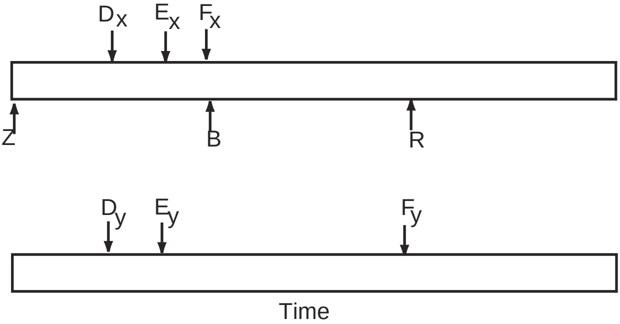


Figure 4.3. Potential complexities in developmental programs for two cell types, *x* and *y*. B = birth; D = time of determination; E = time of genetic expression as a differentiated cell; F = time of full cell function; R = age of reproduction; Z = zygote formation; See text for further explanation.

Even with this simple situation, the possible outcomes are complex. Consider the cases in which the developmental determination events D_x and D_y for the two cell types are interrelated by *developmental constraints* and *functional constraints*. Here, developmental constraints are those where only disruption of the timing of determination causes a reduction of fitness; cell-type x must at least be determined before cell-type y can be determined. In our simple system, cell type x could produce a substance that helps to determine cell type y. Functional constraints necessitate a certain order of cell action. Cell type x might specify a larval protein, which must be present and then loses function before the adult protein is produced by cell type y. Alternatively, events D_x and D_y might have to coincide to function properly. Similarly, function of both cell types might have to be initiated at the same time for proper survival. The various possibilities of timing generate nine possible phenotypes. Imagine a number of traits increasing to the complexity of the simplest of organisms and you soon appreciate the problem of developmental timing in evolution. The degree to which the developmental and functional events D and F interact is the degree to which the phenotype is tightly bound as an integrated developmental system.

The importance of timing is most easily illustrated by relatively simple developmental systems. The cellular slime mold *Dictyostelium discoideum* responds to starvation by initiating an approximately 24-hour program of differentiation. Within 6 hours, cells move toward centers of aggregation, in response to synthesis and secretion of cyclic adenosine monophosphate (AMP). The cells then differentiate into spores and stalks. The developmental program is a sequence of events in which extracellular signals trigger changes in the patterns of gene expression. At each stage, new cellular-surface molecules appear and probably act as mediators for extracellular signals. Removal of the signal responsible for progression from one developmental stage to the next results in the loss of gene products specifically induced at that stage. The ordered expression of genes is affected directly by the extracellular signals, which are high cell density, starvation, cyclic AMP, and the formation of cellular aggregates (Chisholm, Barklis, and Lodish 1984).

The possibility of following the fates of all cells in the nematode *Caenorhabditis elegans* makes it an ideal model system for understanding the consequences of alterations of timing of the transformation of cell fate (Ambros and Horvitz 1984). In certain mutants, cells express fates normally expressed by cells generated at other developmental stages. This can result in precocious or delayed expression of cell lineages that comprise specific body regions or tissues. Alterations in developmental timing can result in the absence or duplication of specific structures, partial sexual transformation, and changes in the number of larval stages (Figure 4.4). Some of the alterations in cell fate transformation may be related to hormonal action on gene expression. Although major transformations most likely have broad-scale negative effects, minor changes may explain directions of evolution. For example, the vulva of *C. elegans* is formed from three cells in the central body region and will not develop unless induced by the gonad. In some nematode genera, however, the vulva is located in the posterior body region. The same precursor cells give rise to the vulva in both *C. elegans* and the posterior-vulva species, but the three cells of the latter species first migrate rearward and do not require induction by the gonad

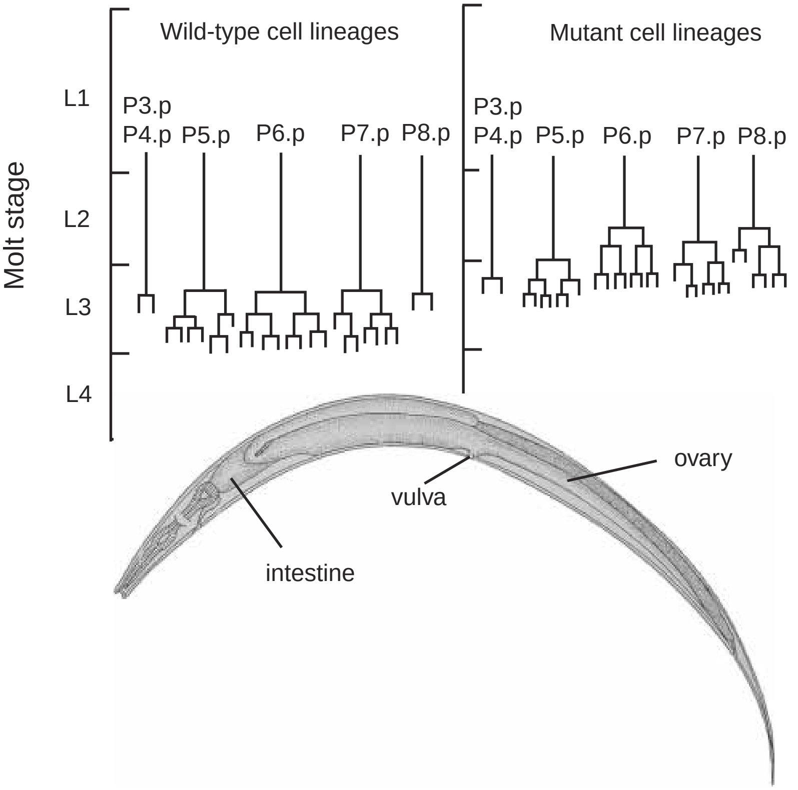


Figure 4.4. Differences in development of cell lineages in wild type and a mutant of *Caenorhabditis elegans.* In the mutant strain, the extra cells generated by P8.p from an ectopic ventral protrusion, which is posterior to the pseudovulva formed by the progeny of P5.p, P6.p, and P7.p. Vulva morphogenesis began at the L2 molt, approximately one larval stage earlier than in the wild type. (After Ambros and Horvitz 1984.)

(Sommer and Sternberg 1994). Thus, evolution of organ position involves changes in induction and competence.

Rate and localization of developmental processes. To understand the developing organism, at least two major components in addition to timing must be studied: rate and localization. The rate of cell division and production of developmentally potent substances, such as hormones, strongly affects timing. In some cases, substances will have varying effects on different tissues; this is a mechanism commonly proposed to alter the relative times of appearance of different structures from phylogenetic ancestor to descendant, one of the commonly accepted definitions of heterochrony.

The relative rates of full expression of traits can have dramatic consequences (Haldane 1932b), which are illustrated classically by the relative rates of development of eye facets and deposition of pigments in the compound eyes of the amphipod *Gammarus chevreuxi* (Ford and Huxley 1927, 1929). Various mutants influence facet color by modifying the rate of pigment deposition. All colored eyes in the adult are colorless at first. This is followed by the formation of a red pigment; facets then darken to near black by the deposition of melanin. In red *rr* eyes, the onset of melanin deposition is delayed and the rate of deposition is decreased. Facets are added throughout life, and later facets, even in normal black eyes, are pale. Mutants with slow somatic growth have a relatively greater amount of melanin deposited per facet, and eyes blacken earlier. Gene expression in the vertebrate limb is strongly affected by high cell division rates of cell lineages whose influence on the early patterning of body plans is mediated through production of morphogens that communicate between cells and in a diffusion gradient (Duboule 1994).

The cell's developmental fate is influenced by its location in the developing organism. This is known as *localization,* a universal phenomenon in development. Contact between cell types causes *induction* (i.e., determination of a new tissue type). Induction may require specific inducing tissue cells. In the vertebrate eye, for example, the optic vesicle will develop only when primordial tissue is placed in proximity with head epidermis. In others, a glass or biological surface induces the same developmental events (Wessells 1977).

Localization is intimately related to the collateral phenomena of timing and rate. For example, the great Swedish embryologist Horstadius worked out the geometrically complex early events in the development of the sea urchin embryo. This morphological work has been supplemented by a more recent understanding of the molecular biology of early sea urchin development (Davidson 1976; Davidson et al. 1982). At fertilization, maternal RNAs dominate but eventually lose their influence over subsequent development, depending on the rate of induction of nuclear genes in the new cells. After the fourth cleavage, four micromeres give rise to, among other cell types, 30 primary mesenchyme cells that invade the blastocoel cavity. Later, the gut tube bends forward across the blastocoel, preceded by strands of secondary mesenchyme cells. Filipodia extend across the archenteron, where they search for the appropriate surface before contracting to cause gastrulation (Gustafson and Wolpert 1961). The mouth is induced where the gut makes contact with the wall of the blastocoel. Like most other embryos, this event is followed by a complex series of movements and inductions, resulting eventually in the development of the adult organism. All morphogenetic movements are controlled by (1) differential cell contraction and expansion and (2) adhesion among cells. Gastrulation is widespread in embryogenesis, even though the details are quite different, which likely indicates that gastrulation evolved many times. This may suggest that there is an internal selection for developmental programs that cause new contacts between cell layers to provide positional information for further development of later structures.

Morphogenetic movements must involve not only induction but also mechanisms for cell kinesis. Presumably, substances that are transmitted from cell to cell induce contraction of microfilaments. Odell et al. (1981) suggested a model for gastrulation by assuming that a small number of connected cells in a sheet are excitable and contract on one side. The cell is modeled as a viscoelastic body whose apical end can be reduced in size by contracting microfilaments, much in the way that a draw string closes a purse. The properties of the sheet can cause an invagination to occur. Some signal in the amphibian egg is necessary to cause a set of localized cells to engage in coordinated contraction. In *Pleurodeles waltl,* the mutant *ascite caudal* shows disturbed epibolic movement during gastrulation (Bluemink and Beetschen 1981). In the early gastrula stage, ectoderm cells begin to sink in at random sites in the animal half of the embryo. In later stages of gastrulation, the ectodermal pits develop into grooves. Electron microscopy shows that many cells in the bottom of the pits and grooves have narrowed apices. This result suggests that some organizing signal has failed to stimulate localized contraction and proper gastrulation.

The complexity of development and the possible morphological outcomes (Figure 4.5) can be understood as the interaction of two sets of developmental components (Larsen 1992). First, cells important in development may effect change by in situ cellular processes (e.g., cell division); alternatively, they may undergo elaborate migrations through several tissues and then act by means of cell–cell communication at the target site. As tissues arise from cell division, the second component involves whether the structure, once instructed, will automatically be elaborated into a further stage of development (autonomous) or whether further developmental patterns will be conditional on specific cell–cell contacts. In either case, a series of structures will be formed from large numbers of cells.

A universal template for animal development. Evidence from *Drosophila* and many other animal species reveals the omnipresence of some DNA sequences involved in development. For example, a controlling sequence, the homeobox, is widespread in animals (McGinnis, Garber, Wirz, Kuroiwa, and Gehring 1984; Muller, Carrasco, and DeRobertis 1984). Such sequences belong to genes crucial in gene regulation and development. The homeobox codes for the 60 amino acid homeodomain family of proteins, which regulate the binding to specific DNA sequences, which, in turn, regulate the downstream expression of genes crucial in the development of major body axes and segmentation (Gehring 1987). Although the DNA sequences regulated by the homeodomain may vary among organisms, a surprising degree of

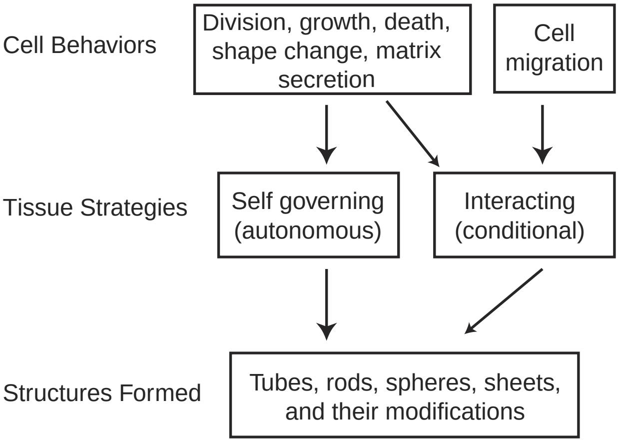


Figure 4.5. Relationship between cellular-level developmental processes and biological structures. (After Larsen 1992.)

homology has been found among a broad range of protostomes and deuterostomes. This suggests conservation of some sequences and developmental patterns for over 500 million years.

Gene function. The roles of genes in development at the molecular level have been examined using the following evidence:

1. *Expression patterns:* In well-understood model organisms (e.g., *Drosophila melanogaster, Mus musculus*), early developmental progressions in regionalization are predictable. Using antibodies, gene products of many developmental genes can be visualized (Figure 4.6). If patterns of expression come and go with specific developmental events (e.g., dorsoventral patterning), then a possible directing role for the gene may be inferred.
2. *Loss of function:* In the well-studied mouse and fly, mutants of specific genes can be shown to lose function. The associated effects of development can be inferred to be related to such losses. This is a principal means by which anteroposterior patterns in gene expression were first understood for *Drosophila* (Lewis 1978). Gain of function can also be studied by, for example, insertion of appropriate mRNAs into specific tissues.
3. *Targeted loss of gene expression:* In mice, it is possible to knock out expression of specific genes, giving one the opportunity to examine effects on development. Such knockouts are also possible in flies.
4. *Implantation of mRNAs and other developmentally active substances:* The restoration of gene function can often be studied by knocking out a gene's activity and implanting mRNAs from another organism. In some cases, developmental genes can set in motion autonomous developmental events in any place where the transplant occurs (ectopic expression). Transplants between distantly related species can give an inkling of the universality of gene function in a given developmental process.

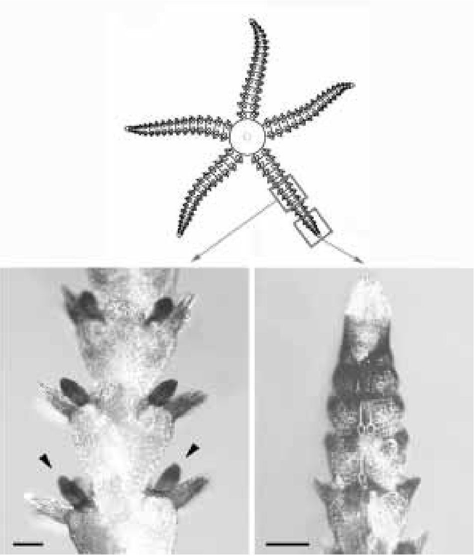


Figure 4.6. Expression of the epidermally associated orthodenticle gene in two regions of the brittle star *Amphipolus squamata.* Lower left shows expression areas on the middle arm of a juvenile, whereas lower right shows expression at the tips. (Courtesy of Gregory Wray.)

Developmental gene types. The main picture that emerges from molecular developmental studies is this: A highly conserved set of genes that control development have been recruited into many specific developmental functions. The same gene (e.g., *Pax-6, engrailed* in flies) is usually found expressed in different regions of the developing animal or at different stages in development, suggesting a multiplicity of uses for the same gene product. This is not to say that the specific role of the protein varies. A transcription factor is always such; it just performs this role in different contexts, switching on different batteries of genes to set into motion different developmental pathways. For example, the *Notch-Delta* protein can be found expressed in the central nervous system, in competent muscle cells, in bristle patterning, and in the oocyte follicle (Gerhart and Kirschner 1997).

Developmental gene products include the following types:

1. *Transcription factors:* These factors best approximate Britten and Davidson's notion of integrator genes that initiate batteries of gene expression that guide developmental events. In effect, this part of the transcriptional apparatus acts like the gunshot that begins the race. Along with RNA polymerase, eukaryotic genes require the binding of transcription factors, often many, for gene transcription to commence. These are bound to DNA, and the genes responsible may be distant from the RNA polymerase binding site (Gerhart and Kirschner 1997). Some factors, for example, can suppress gene expression by occluding the binding site for RNA polymerase. Proteins bound to the DNA react with arriving transcription factors to affect transcription.

   The starting gun in a race may not be a completely appropriate metaphor, even though it does appear that transcription factors initiate a cascade of events leading to expression of other genes. Current research in developmental biology tends to look for universal and immutable roles of such factors. Studies of the nematode *Caenorhabditis elegans,* however, demonstrate some distinctly different roles for the Hox gene transcription factor *mab-5,* the worm homologue of the *antennapedia* gene in *Drosophila melanogaster.* Expression can be seen in the posterior during development, but its expression is more controlled by stage in a cell lineage than by spatial location. The gene cannot be induced alone by position in the body. Furthermore, the gene is not a one-off initiator of developmental events, but its expression is turned on, off, on, and off and plays multiple roles in the initiation of cell division cycles. It is likely that such programs are widespread, despite the superficial appearance of spatial designation and early singular expression. This demystifies the apparent early "master switch" control of these genes in early development.
2. *Cell communication factors:* Here, a signal protein makes contact with a specific receptor at the cell surface. The range of signaling molecules and receptors is immense, but all basically involve the setting off of a cascade of reactions within the cell, causing or enhancing expression of specific nuclear genes. The activity of such communicators (e.g., *hedgehog* and *wingless* in *Drosophila*) is strongly regulated by cell surface receptors.
3. *Receptors:* These proteins are part of the cell membrane and bind to cell communication factors. More rarely, they are in the cytosol. They work in conjunction with *signal transducers,* molecules that carry a signal from a receptor to a site of important activity, such as initiating cell division or transcription.

4. *Diffusible morphogens:* Soluble diffusible factors affecting development were first predicted by theoreticians (Meinhardt and Gierer 1974; Turing 1952), but several molecules have now been identified as necessary for development. A *morphogen* is produced by a group of cells and diffuses over a distance, which cannot be passively dispersed much more than 1 millimeter in a rapidly developing organism. For example, the array of vertebrate digits is determined by polarizing signals from the *zone of polarizing activity* (ZPA). Retinoic acid (RA) is the polarizing molecule that determines posterior-to-anterior expression, which works in conjunction with *sonic-hedgehog* (vertebrate homologue of *Drosophila hedgehog*) to determine anteroposterior digit formation (Riddle, Johnson, and Laufer 1993). One can get ZPA-like activity by adding RA beyond the usual distance over which the morphogen acts (Helms, Thaller, and Eichele 1994). Other genes are stimulated into action when receiving certain concentrations of the diffusible morphogens. Morphogens need not be restricted to a role as diffusible substances. The *Drosophila hedgehog* can be a cell-to-cell communicator, but with the action of a membrane-active gene, *tout-velu, hedgehog* instead becomes a diffusible substance, acting over many cell diameters (Bellaiche, The, and Perrimon 1998, and well discussed in Ingham 1998).

Developmental genes involved in spatial patterning have the following classes of effects:

1. Determination of major embryonic spatial patterns (anterior versus posterior, dorsal versus ventral).
2. Determination of polarity within smaller units, such as within segments or other localized repeated structures in insects.
3. Determination of anterior and posterior endpoints of an otherwise quasi-segmented body plan.

Gene function, development, and evolutionary change

Axial patterning genes. The study of developmental biology has been revolutionized by the discovery of the functioning and significance of DNA-binding homeodomain proteins of 60 amino acids, which are widespread yet highly structurally conserved in animals (Gehring 1987; McGinnis, et al. 1984; Muller et al. 1984). Despite structural similarities, sequences often differ substantially. A surprising degree of homology, however, has been found among many animal phyla, suggesting conservation of homeodomain DNA-binding functions for over 500 million years. Although homeodomain proteins may bind to a broad variety of genes, they are quite specific in action when combined with other transcription factors. They therefore must work in conjunction with other binding factors to effect specific developmental events. With the interaction of different transcription factors, homeodomain proteins act in different contexts to activate batteries of different developmental gene systems.

Genes with homeobox sequences (coding for homeodomain proteins) are widespread in animal genomes. But a conservation of gene action was discovered that was even more startling than the conservation of homeodomain protein structure and sequence homology. A set of *Drosophila* genes with homeodomains, the *Hom-C* genes, could be aligned to a similar set found in vertebrates, the *Hox-C* genes (Figure

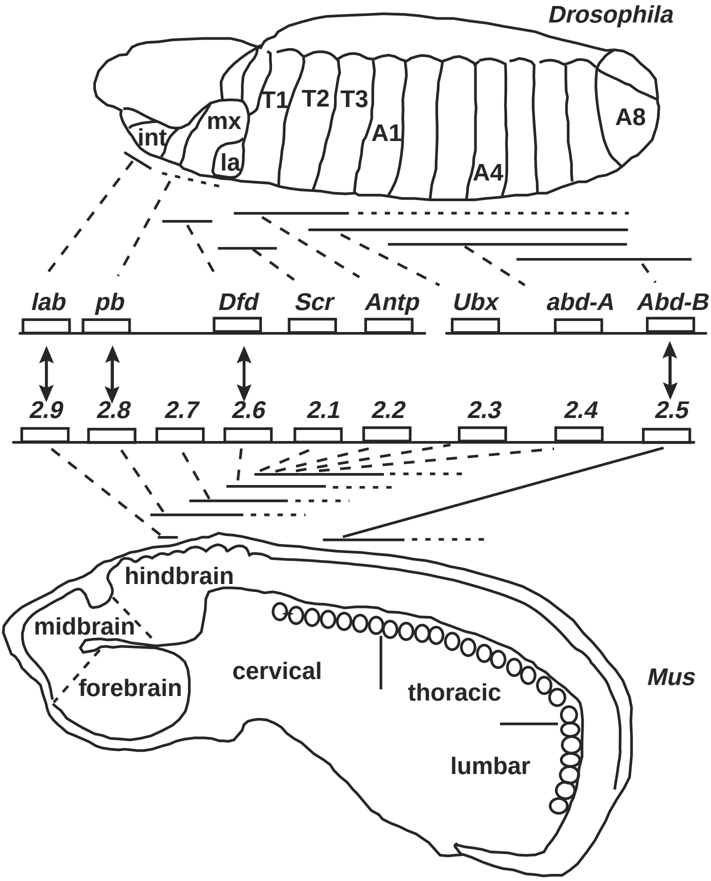


Figure 4.7. Alignments and domains of expression of the set of *Hom-C* genes in *Drosophila* with the four *Hox-C* sets found in vertebrates. Dashed brackets indicate uncertainties of matching between fly and mouse. (After McGinnis and Krumlaf 1992, © 1992, Cell Press.)

4.7). In both these cases, the genes regulated axial patterning in early development. The order of genes on the chromosomes, moreover, corresponded to the anteroposterior expression of these genes. Suddenly, it became possible to believe in a master set of genes that controlled early development identically throughout the animal kingdom. The universality of these sequences is, as mentioned above, to be contrasted with their multiplicity of uses in development in other contexts. Thus, in all cases, we are confronted with a problem. Is the developmental toolbox a source of conservation in evolution or a nearly boundless opportunity for developmental diversity?

Our understanding of the *Drosophila* system began with the discovery by Nobel laureate Edward Lewis (1978) (following work earlier in the century by Calvin Bridges) that a grand scheme of anteroposterior determination could be localized in the eight-gene *bithorax* complex, which appeared to code for substances controlling levels of thoracic versus abdominal development. The outcome of failures of gene expression resulted in anteroposterior transformations, known as *homeotic mutants*. This is discussed more below (under Homeotic Mutants and the Master

Switch Theory), but the important point to appreciate is *bithorax*'s control of axial patterning, which was established early in development. *Drosophila* is a so-called long-germ-band insect, meaning that segment identity is established by the blastoderm stage. Later discoveries of other homeotic genes, such as *antennapedia,* only strengthened the hypothesis that a set of major genes were responsible for axial patterning and other important aspects of development.

Crucial studies by Nobel laureates Nüsslein-Volhard and Wieschaus (1980) demonstrated that developmental gradients from the largest scale of whole-body gradients to those between cells were crucial in the determination of segment patterns in fruit flies. By the enumeration and examination of segmentation mutants of fruit flies, they found that the early establishment of segmentation is followed by patterns affecting alternating segments, which in turn is followed by the establishment of gradients within segments.

Overall, the expression patterns of the *Hom-C/Hox-C* (*Hox*) genes suggest that anteroposterior axial determination at any one location derives from interactions of expression domains of at least two genes (Figure 4.7). Thus, thoracic segment identity is explained at least by interactions between *Ubx* and *Antp*. Polarity of segment determination in fruit flies is also influenced by the protein products of the *wingless* and *hedgehog* genes, which feed back on each other and help to determine parasegment boundaries. The wingless gene further influences expression of *engrailed,* another crucial gene in axial patterning (see Ingham 1994). These discoveries fit well with the morphological observations (Lewis 1978) that demonstrated homeotic switches of developmental fate, converting posterior segments to those with the morphology of anterior segments. Although the *Hox* genes act to set body patterning in motion by determining embryonic regions, other proteins act in specific determinations of segment number and identity.

It soon became apparent that the fruit fly *Hom-C* genes were active in determining many aspects of segment identity, number, and various intra- and intersegmental pairings of traits (Akam 1987, 1989). The eight genes can have different fates in gene expression, depending on the action of different promoters and differential splicing of messenger RNAs. Importantly, the function of these genes was abstract; they could set off the expression of batteries of genes in many developmental contexts (McGinnis and Krumlauf 1992). It is therefore an easy jump to argue that transcription factors could be recruited into many developmental systems independently. But could this be so for the axial specification genes? After all, gene order is more or less conserved between flies and mice, suggesting that regional anteroposterior differentiation is an ancient evolutionary innovation, retained since before the protostome–deuterostome ancestor. The alternative hypothesis would be convergence, but it is hard to accept that colinearity of gene action between flies and mice is entirely coincidental, generated by evolutionary convergence. As an alternative, it might be that there is lability in the regulation of gene expression to some small degree but that the axial patterning would be severely disrupted if gene order and action had changed substantially. The conservatism of these gene orders over broad evolutionary distances may suggest that normal development would be far less efficient or perhaps completely chaotic unless the gene order is retained.

Dorsoventral patterning. In *Drosophila,* dorsoventral patterning also operates under the control of transcription factors but relatively independently of the axial system. Distinctive gene expression patterns can be found as early as the blastoderm embryo. Whereas axial genes are expressed in regions in both mesoderm and ectoderm tissues, dorsoventral patterning genes may be expressed only in single tissues. As in axial patterning, strong conservation of gene action has been found, between the usual fly and mouse models. Only something is quite different, to say the least.

In *Drosophila,* the gene product of the maternal gene dorsal affects gene expression of dorsoventral patterning genes, most of which are expressed in the dorsal embryo. The genes initiate the expression of *decapentaplegic* (*dpp*), which sets up a diffusion gradient ventrally that is antagonized by another factor, *short gastrulation* (*sog*), which is produced ventrally and diffuses dorsally. In *Xenopus, Xenopus chordin* (*chd*) appears to be homologous to fly *sog.* The gene *bone morphogenetic protein* 4 (*Bmp*-4) appears to be homologous to *dpp.* It is expressed ventrally, and implantation of the gene product dorsally will convert dorsal mesodermal cells to ventral fates (DeRobertis and Sasai 1996).

If the gene expression in dorsal and ventral regions is taken to be homologous, then a vertebrate is a protostome upside down (Figure 4.8). Nübler-Jung and Arendt (1996) marshal a great deal of morphological and molecular evidence to support this view. This is precisely what Geoffroy Saint-Hilaire argued in the early nineteenth century, although it has been rejected, proposed, and rejected again (Nübler-Jung and Arendt 1996). Dorsoventral homology has been fodder for large-

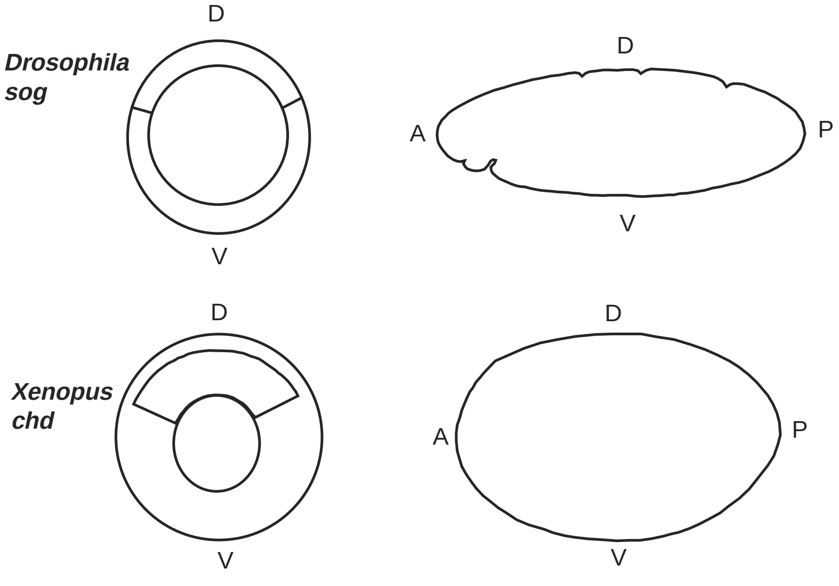


Figure 4.8. The expression of fruit fly *sog* (top) and clawed toad *chd* (bottom). Note the dorsoventral reversal of expression. Blastodermal expression at left; end of gastrulation at right. (From DeRobertis and Sasai 1996; reprinted with permission from *Nature,* © 1996, Macmillan Magazines, Ltd.)

scale debates about evolutionary relationships, so this result appears to rule in favor of homology as the reason for the spatial relationships between the gut (below in vertebrates, above for protostomes) and the central nervous system (above for vertebrates, below for protostomes). Because the gene systems mentioned are responsible for regional dorsoventral patterning, we do have to take seriously the possibility that the expression patterns may reflect a change in dorsoventral directional patterning before the rise of the vertebrates. It appears that DeRobertis and Sasai (1996) safely excluded some other possibilities, such as more complex dorsoventral determination mechanisms and lack of homology of the fly-toad genes. It is easy to get excited about this, but remember that we have only two species here, with the possibility that more study will produce complexity. Also, our current knowledge fails to answer obvious questions, such as: Might there be a functional reason why the reversal occurred? The coincidental evolution of the vertebrate central nervous system with the axial skeleton (both dorsal) comes to mind. But if that were true, then what about the functional morphology of the tadpole larva of ascidians: Does that require a dorsalization of nervous system and skeletonization? One also has to consider the possibility of convergence of use of these patterning genes. Before we flip over this, we will need a better and more phylogenetically complete data set that can be used to trace the exact evolutionary pattern of dorsoventral differentiation.

Nielsen (1999) argued that the chordate neural tube arose through lateral fusion of a ventral, post-oral loop of the ciliary band in a dipleurula larva. The stomodeum could move from the ventral area to the dorsal side, which faces the substratum in chordates.

Other patterning. It is not my intention to catalogue the complete set of spatial patterning genes that have been discovered. There are at least 100 transcription factors active in early development, beyond the 10 *Hox/Hom* genes. Proximodistal patterning, for example, is often controlled by the *Distalless* gene, which in flies is important in the growth of appendages.

Switching on Developmental Events

Homeotic mutants and the master switch theory. Because some developmental fields can be relatively independent of others and because such a field may consist of a few embryonic cells at the time of its origin, which might be subject to strong changes, it seems likely that major changes in developmental fate might be induced by a change of developmental instructions. Such seems to be the case in the renowned *homeotic mutants,* which are defined as variants with alternative differentiative capacity. Recent discoveries suggest that such mutants are one of a class of selector genes, each of which acts as a binary switch to turn on a developmental sequence. This leads to the question of considering evolution as a series of major revolutions as various evolutionary master switches evolve. There is an alternative, however. It may well be that a switch is required to efficiently set a developmental sequence in motion, but the switch may be more like the firing of a gun at a race, meaning it would work just as well at an automobile race as at a human footrace.

Getting the car, or the runner, to work correctly is a complex series of processes that "evolved" independently of, and perhaps before, the gunshot.

The *bithorax* complex of *Drosophila melanogaster,* the best-studied series of homeotic mutants, was first discovered by Calvin Bridges in 1915. Lewis (1963) found that eight complementation groups explained the total variation. In fruit flies, as in other Diptera, the mesothorax bears the second pair of legs and the single pair of wings. The third pair of legs and halteres are found on the metathorax, and the first abdominal segment lacks appendages. *Bithorax* mutants alter this arrangement. Apparently, the form of the second thoracic segment is a sort of ground state, as mutants tend to alter the fate of more posterior segments toward this form. *Ultrabithorax,* for example, converts the third thoracic and first abdominal segments into second thoracic segments (it is lethal in the homozygote). The interaction of alleles at the eight loci is complex and not fully complementary, but there seem to be two major independent domains, whose boundary lies within the first abdominal segment (Struhl 1984). Major switches of development are common in most mutants. These must be associated with switches of determination at the time of segment formation. The effects have polarity, because mutants affect segments posterior to the second thoracic and not anterior.

The mutants seem to be the result of major alterations in the genome that apparently affect development quite severely (Bender et al. 1983). The mutant *bithorax* (first abdominal → second thoracic) is associated with the mobile repetitive element *472,* wheras *bx34e* is associated with the mobile element *gypsy.* In other cases, large lesions of up to 73,000 base pairs (of the 195,000 base pairs investigated) are the cause of the mutants. Homeotic mutations are also common in other arthropods. The cyclops mutant discussed above in the brine shrimp *Artemia salina* is a good example. To a lesser degree, such variants can also be seen in vertebrates. The *ametapodia* mutant in the chicken causes the wing to develop approximately as a leg (Cole 1967), but no vertebrate system shows the simple switches characteristic of the arthropods.

How do switches arise? Potential complex relationships between switch genes, their downstream targets, and functional considerations can be illustrated by the formation of the developmentally arrested dauer larva stage of the nematode *Caenorhabditis elegans* (Riddle, Johnson, and Laufer 1981). Normally, the larva passes through four molt stages, but overcrowding or starvation causes entry into the dauer larva in the second. The duration of the dauer stage does not affect subsequent longevity. Studies of mutants suggest that the genes responsible for induction of the dauer stage are ordered in a pathway and that the order corresponds to neural processing of environmental stimuli necessary to stimulate the developmental switch. Two of the mutant genes are correlated with chemotaxis defects, and both mutants exhibit ultrastructural alterations in specific neurons that have previously been implicated in the chemosensory response to salts.

The induction of the dauer shows the intimate relationship among genes, developmental order, and selection. We do not know how the sequence was built up in evolution, but the disruption of a gene's function probably affects the internal organization of the order of gene action, interaction between neurosensory substances, the establishment of neuronal pathways, and the ability to monitor the external environment for the proper cue to enter the dormant state. Some dauer mutants, however, can sidestep any interaction with the external environment. The *dauer constitutive* mutants switch on the dauer larvae stage, irrespective of crowding and food conditions. This suggests that once a developmental pathway is integrated, probably by natural selection in this case, it can then be incorporated into the internal organization of the genotype and phenotype by means of the recruitment of a selector gene such as dauer constitutive. One can imagine a harsh seasonal environment in which the dauer larva is no longer an option; the developmental pathway becomes fixed by selection and incorporated into development.

The switch to dauer formation is apparently controlled by the gene *daf*-18, which is a component of the insulin-like signaling pathway. The gene controlling entry into diapause and adult longevity is regulated by the *DAF*-2 receptor tyrosine kinase and the *AGE*-1 PI 3-kinase. Others have shown that mutation of *daf*-18 suppresses the life extension and constitutive dauer formation associated with *daf*-2 or *age*-1 mutants (Roualt, Kuwubara, and Sinilnikova 1999).

The dauer larva suggests the following ordering of evolution: Complex gene interactions accumulate during the course of evolution in order to specify a complex system. In the case of the dauer larva, this involves sensory connections with the external environment combined with a battery of genes that must specify the resting dauer larva. This seems like a sensible model for the evolution of development, which can be extended to other developmental genes. Or can it?

The *Pax*-6 gene is a good example of a switch gene. Its "master control" status is supported by similar eye development activation in phylogenetically vastly distant clades (including primates) and strong sequence homology, including similar splice locations. But the great differences in eye structure among vertebrates, mollusks, and arthropods, for example, suggest that there must be a large part of the genome that is differentiated among these groups to specify eye development. One is left wondering about the evolution of function of the gene itself, which might have been recruited in many clades independently to switch on eye development (Dickinson and Seger 1996). The implantation of mouse *Sey* gene or the *Pax*-6 gene from a squid, *Loligo opalescens,* into *Drosophila* results in expression of ectopic eyes (Figure 4.9) with a remarkable degree of completeness (Halder, Callaerts, and Gehring 1995a, 1995b; Tomarev et al. 1997).

Is there a prototypical eye gene? If so, there must be a fixed prototypical gene set, associated with *Pax*-6, of visually related functions that antedate the divergence of the triploblasts and even the diploblasts. This set, downstream of the effects of *Pax*-6, must show the same degree of homology and types of expression as *Pax*-6. Then and only then can we be satisfied that there is such a thing as a prototypical eye or at least a prototypical vision system, on which other structures are connected, depending on phylogenetic affinity. The evidence does, however, favor the ancient nature of *Pax*-6. It has strong sequence homology in many phyla and even conservation of splice sites in vertebrates, arthropods, and other phyla such as ribbon worms and ascidians (Glardon, Callaerts, Halder, and Gehring 1997; Loosli,

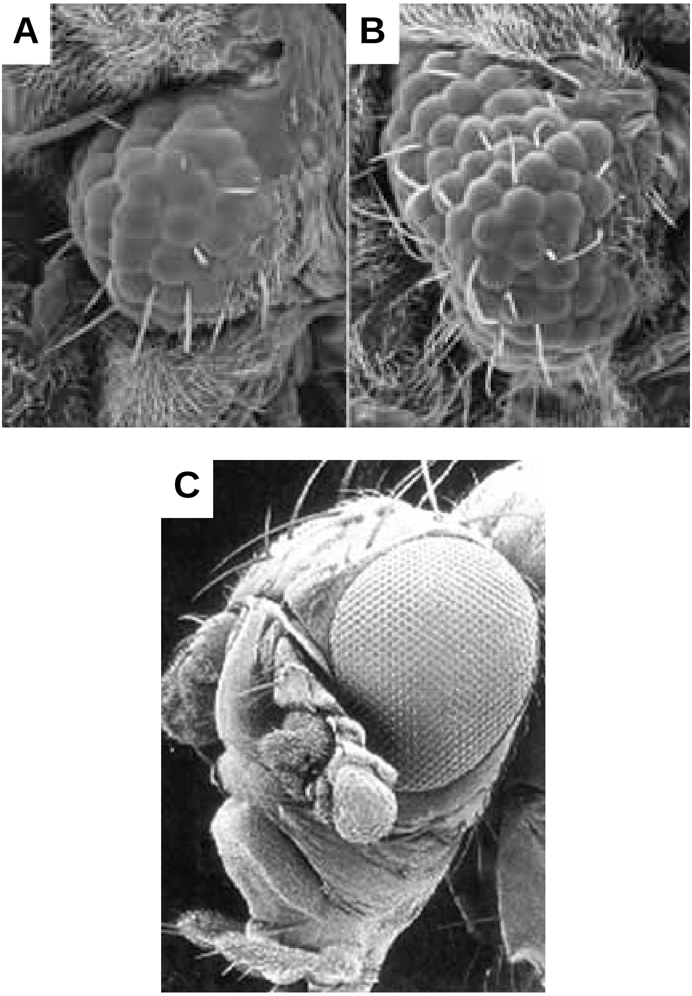


Figure 4.9. (**A** and **B**) Ectopic eyes induced by application onto fruit flies of mRNAs; (**C**) products of the *Pax*-6 gene from the squid *Loligo opalescens.* (From Tomarev et al. 1997 with permission; © 1997, National Academy of Sciences USA.)

Kmitacunisse, and Gehring 1996). The larva of the sea squirt *Phallusia mammillata* has a simple photosensitive ocellus. *Phallusia Pax*-6 shares extensive sequence identity and conserved genomic organization with the known *Pax*-6 genes of vertebrates and invertebrates. At the tailbud stage, *Pax*-6 is expressed in the spinal cord and the brain vesicle, where the sensory organs (ocellus and otolith) form, suggesting an important function in their development. Again, we are compelled to see *Pax*-6 as a pananimalia vision-controlling gene, perhaps as ancient as the origin of animals.

Gehring (1996) argued that the *Pax*-6 gene is a phylogenetically conserved master gene. The ubiquitous presence of opsins in animals and the conservation of their use in light absorption suggest a *Pax*-6 connection to switching on this ancestral part of the vision system, which may be connected to vision systems in various phyla in a variety of ways. Here it is argued that the master may have evolved first (Halder et al. 1995a, 1995b). Maybe he's right, but information is too incomplete to judge. After all, *hedgehog* homologues function in the generation of wings in insects and birds. Can one seriously argue that this is a wing master gene, connoting a universal wing system in the animals (Dickinson and Seger 1996)? At this stage, it seems most parsimonious to conclude that sometime in animal history the *Pax*-6 gene became intimately linked with opsin and forevermore initiated development in visual systems. It is equally likely, however, that the evolution of eyes in different and complex ways occurred independently in many phyla.

It would be of interest to know whether *Pax*-6 is shut off in those organisms that lose eyes as they invade lightless environments. Many cavefish appear to have a gradual loss of eye structures, rather than a complete loss, which would be expected from the master switch theory. In blind populations of the cavefish *Astyanax mexicanus,* the *Pax*-6 is downregulated in the developing lens (Jeffery and Martasian 1998). The cavefish develops an optic primordium, but the early developing eye ceases to develop and degenerates. Thus, alterations in lens development are crucial in the loss of eyes, which is consistent with previous knowledge of eye development by means of tissue induction. It may be tempting to see *Pax*-6 as the giver and the taker of eyes, just at the flip of a switch. But this is not true: There is good evidence for the role of multiple genes in eye degeneration and for different genetic patterns in different *A. mexicanus* populations (Wilkens 1988). One wonders if the genes involved in reduction of eyes are the very same genes that construct the eye in sighted populations; this makes sense and is evidence for the multigene constructive role for visual morphological systems. It is reminiscent of the dauer mutant in *Caenorhabditis elegans.*

Organization, Compartmentalization, and Restriction in Development

Compartmentalization, developmental fields, and organization. If the evolution of developmental programs is constrained to produce combinatorial states of developmental units, then it is important to learn the degree of autonomy of different developmental units and the difficulty of evolving the breakup of the units. Until the 1990s, such information was difficult to obtain because the spatial relationships could be understood only with reliable cell markers permitting a sequential mapping of cell fate. Now that the molecular study of development has come onto the scene, it has been possible to understand developmental mechanisms by studying spatial patterns of gene expression and function.

The simplest case of autonomy of regions would occur in embryos in which individual regions are easily identified and autonomous and are relatively incapable of switching their ultimate fate as differentiated structures. The classic case of such development is found in holometabolous insects such as *Drosophila,* where the adult structures of the imago derive from imaginal discs, divided into nine pairs plus one. The discs are pouches of epidermal cells that differentiate at the terminal molt, and each produces specific structures in the adult fly. For example, one pair gives rise to antennae and eyes, another develops into some of the abdominal structures, and yet another three pairs form the legs.

The fate of the imaginal discs is determined early and is difficult to change. Serial transfers of imaginal discs can be done repeatedly between flies with low titer of ecdysone (Hadorn 1967), but the ultimate fate of the disc does not usually change. Occasionally, however, *transdetermination* of a given disc type to that of another occurs. Transdetermination is a quantum process; intermediate disc types are not found and the pathways of conversion from one disc type to another are predictable (Hadorn 1967; Figure 4.10).

Autonomy of developmental regions in insect wing development demonstrates the potential nature of independence of developmental units. *Compartments,* found in *Drosophila* and other arthropods, are areas of epithelium bounded by special demarcation lines (Crick and Lawrence 1975; Garcia-Bellido 1975; Garcia-Bellido et al. 1973). They are formed from the descendants of a small number of founder cells and their fate is determined by "selector genes" (Garcia-Bellido 1975). Compartment boundaries were identified by inducing somatic mutants with x-rays at various times during development and by following the subsequent fate of cell clones on wings. Cell clones become successively restricted in potential as development proceeds and are marked by the appearance of a regular sequence of boundaries across which the clones will not trespass. As development progresses, a major compartment is successively divided into smaller and smaller compartments. The wing compartment boundaries are determined by some spatial signal. Differential cell division rates do not affect the ultimate shape and size of a given compartment.

Segmentation in insects is also determined by a compartmentalization process, where boundaries are determined by successive actions of genes affecting segment boundaries. During development, a succession of gene actions determines the anteroposterior axis, segment identity, and polarity within segments. In the milkweed bug *Oncopeltus,* segmentation is defined between the late blastoderm and early germ band stages. Each segment is a unit of a cell lineage and develops from a small group of founder cells set aside in the embryo (Lawrence 1981). In *Drosophila* embryos, segmentation is being set up in the blastula stage; segmentation is first visible one hour after the onset of gastrulation as a repeated pattern of bulges in the ventral ectoderm (Nüsslein-Volhard and Wieschaus 1980). Before true segments appear, a set of parasegments can be defined at the blastodermal stage, which are nearly spatially coincident with true segments. Parasegments can be defined by expression pat-

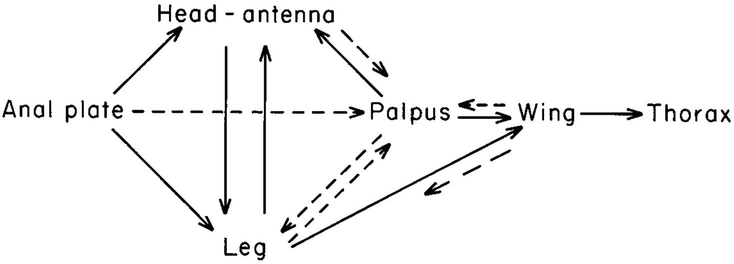


Figure 4.10. Transdetermination pathways of *Drosophila* imaginal discs. Rare changes designated by dashed lines. (After Hadorn 1967.)

terns of early developmental proteins such as the product of the gene *engrailed*. The parasegments are compartments that can determine further development within the parasegment and respond to larger spatial scale developmental signals. Within each segment, other developmental phenomena may determine arrangements of structures such as surface features of the cuticle (Lawrence 1981; Locke 1959; Locke and Huie 1981; Nüsslein-Volhard and Wieschaus 1980).

The concept of compartments in insects can be generalized to other organisms as *developmental fields* or regions of strong presumed developmental interaction, relatively independent of other regions. Such dependency has long been known to be important, at least as a morphological correlation. *Pearson's rule* states that correlations among body parts are stronger with increasing proximity (e.g., Sokal 1962). In mammalian tooth development, for example, correlations between measurements in adjacent teeth are often better than in distantly located teeth (Kurtén 1954). In humans, absence of the third molar is correlated closely between right and left sides but uncorrelated between upper and lower jaws (Garn, Lewis and Vicinus 1963). The reappearance of the metaconid–talonid dental complex in the lynx, long lost in the annals of cat history, seems correlated with the reappearance of the second molar (Kurtén 1963). Some evidence also exists for a correspondence between dental developmental fields and order in development, as in the phenomenon of compartmentalization found in insects. Tooth genesis and eruption order is stereotyped in mammals. Polymorphisms in sequence, however, are known to occur. In cases of third molar agenesis in humans, the eruption sequence P2M2 is the usual case, as opposed to the ancestral eruption sequence M2P2.

The spatial scale of the effects of diffusion of morphogens suggests that major effects within a developmental field can occur over only short distances. Longer-distance effects might be determined by cell–cell communication systems, modulated by a transmembrane protein (Bellaiche et al. 1998). Localization occurs most effectively in early small embryos, which can be divided into major realms determined by reactions of cell membrane proteins to diffusible morphogens and by cell–cell communication, again mediated by cell membrane proteins. These proteins act as gateways to communication to gene action or changes in metabolism within the cell. As the body increases in size, diffusible morphogens and cell–cell communication could affect only progressively and proportionally smaller regions of the body. Thus, there is a readily understandable mechanism in growing embryos for the progressive restriction of developmental fate of the descendants of a small group of cells.

The homologous relationships between *Hom-C* and *Hox-C* genes in arthropods and vertebrates suggest a compartmentalization process in all animals. One does see some developmental phenomena in vertebrates that can be associated with the concept of segmentation in flies, but there is no distinct set of homeotic genes quite as discrete in effect as those in fruit flies.

Evolutionary lability of developmental organization. Although segmentation domains are well understood, they do not suggest a rigidity that would promote an unbreakable constraint on the development and evolution of insect form. *Drosophila* is a so-called long-germ-band insect, meaning that segment identity is determined by the blastoderm stage. But short-germ-band insects, such as the grasshopper *Schistocerca americana,* generate most or all of their metameric pattern after the blastoderm by sequential addition of segments. The important developmental gene *engrailed* is expressed initially in the fly blastoderm in alternating segments, as controlled by the *even-skipped* gene. But expression differs substantially in the grasshopper, where *engrailed* expression stripes appear singly as the embryo elongates. The *even-skipped* gene does not enforce a pair rule in the grasshopper, as it does in the fly, although it is expressed in early development.

In three beetle species and *Drosophila, even-skipped* is expressed as a pair-rule; the anterior margins of *even-skipped* pair-rule expression stripes mark the anterior border of odd-numbered parasegments, and secondary stripes align with *engrailed* expression stripes. But the cellular details differ substantially. Importantly, the variation observed in germ-band types does not necessarily reflect the gene-expression patterns related to segment identity. During neurogenesis, however, *even-skipped* seems to express in a similar pattern in both *Drosophila* and *Schistocerca* (Patel, Ball, and Goodman 1992). Overall, it is fair to say that there are strongly conserved patterns of gene expression combined with instances of recruitment of genes into new functional relationships (Patel 1994). This is sounding more and more like traditional arguments about morphology! Indeed, although getting closer to the genes gives comfort to those concerned about developmental mechanisms, it does not lead to a sudden universal answer to the question of strict animal-kingdom-wide underlying controls of morphology, let alone morphological complexity. The fundamental gene *bicoid,* discussed above, has no apparent role in setting up anteroposterior polarity beyond those members of the derived Diptera. In fruit flies, the gene *hunchback* can operate to determine thoracic segment identity in the absence of *bicoid* activity. The normal direct regulation of *bicoid* by *hunchback* probably arose recently within the history of the Diptera and is not a fundamental developmental program entrenched in all bilaterians (Wimmer, Carleton, Harjes, Turner, Desplan 2000). Beyond the universality of *Hox,* we find something that resembles a bag of socks.

Expression patterns of *even-skipped* and *engrailed* in insects of quite different early body-patterning strongly suggest that there is no strong conservation of developmental pattern or even of early gene expression, which, after all, sets up the fundamental patterning of body plans (Patel, Condron and Zinn 1994). Thus, the remarkable conservation of the *Hom-C* and *Hox-C* genes masks a great deal of malleability between related species and cannot be used as a means of asserting a fundamental centripetal force in morphological evolution. The genes are the musical notes but the tunes can clearly change.

The sense of great lability in evolution is strengthened by patterns of *Hox-C* gene presence and regulation among the arthropods. Eight *Hox* genes in *Drosophila* regulate anteroposterior axial position, suggesting the possibility that fewer are required in ancestors, especially those with little differentiation among segments. But despite the reduced segmental diversity in ancestrally placed myriapods and onychophorans, all fly *Hox* genes are present in these groups (Figure 4.11). The two fly *Hox* genes *Ultrabithorax* and *abdominal-A,* present in all three groups mentioned, could not have been a trigger for the segmental specialization of dipterans

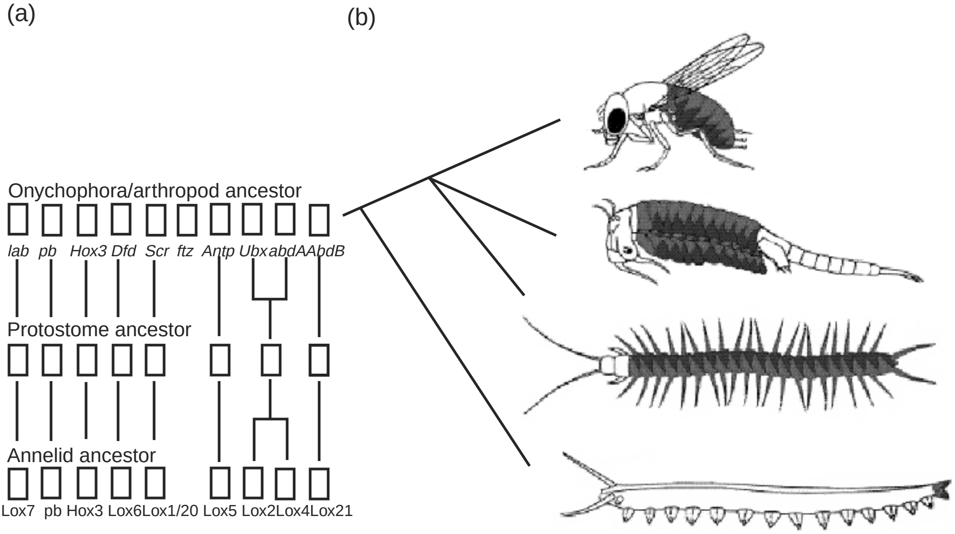


Figure 4.11. Hox gene evolution in arthropods and relatives. *Drosophila, Artemia,* a centipede, and an onychophoran all share the same *Hox* genes, casting suspicion on the idea that *Hox* genes alone are sufficient for segment specification. Annelids and arthropods have evolved a pair of *Hox* genes by means of duplication. The expression patterns of *Ultrabithorax* (black) and *abdominal-A* (shaded) are shown at right.

(Grenier, Garber, Warren, Whitington, and Carroll 1997). Indeed, a marked difference in the expression pattern of *Ultrabithorax* and *abdominal-A* in a centipede and an onychophoran suggests that their trunk segments are differentially determined. The anterior expression boundary of these two genes has changed substantially. The shift in regulation may have involved change in the regulation of *Hox* genes or by changes in segment number. It is quite clear that it is incorrect to attribute revolutionary qualities to *Hox* genes. It is, moreover, incorrect to believe a model that incorporates a revolutionary change, followed by a developmental constraint. The evidence, as limited as it is, suggests a plethora of regulatory mechanisms to produce a great variety of morphologies, whose relationships change like waves washing over a beach.

And change they can, in the most fundamental of developmental unfoldings. All evolutionary biologists agree that the regulation of sex chromosome expression is fundamental in development of sex traits, obviously, but it also affects gene expression of sex genes, where a plethora of genetic messages regulate all aspects of development and metabolic function. In the familiar XX-XY sex determining system, a system must exist to instruct the organism to develop into the appropriate sex but also to express the genes properly, given that one sex has a double dose of genes (XX) relative to the other (X). It should be no surprise, therefore, that a master switch gene exists to determine sex. In *Drosophila melanogaster, Sex-lethal* (*Sxl*) performs the function of female determination when message from XX stimulates the promoter *Pe,* which activates in the blastoderm stage. And so the process continues in a cascade to enable development to a female (Estes, Keyes, and Schedl 1995).

One might think *Sxl* to be a candidate for universal employment to determine sex, but this is not the case, even within the Diptera. Early embryos of the Mediterranean fruit fly (medfly), *Ceratitis capitata,* express the same mRNAs and proteins in both males and females. A sex-determining signal in the medfly has no effect on sex determination, when it is expressed in fruit flies (Saccone et al. 1998). The *Sex-lethal* gene is highly conserved in sequence, and yet its function is clearly different. In the house fly, *Musca domestica,* a switch gene is known to determine sex, but it is not the *Sxl* gene, whose *Drosophila* homologue is expressed in house flies but almost certainly performs another function, perhaps a more minor role in sexual development.

The most parsimonious explanation of this variation is that *Sxl,* long present in the history of the Diptera, was co-opted into the function of a "master switch" gene determining sex during the evolution of the Drosophilidae, and perhaps independently in some groups yet to be investigated. We have clear evidence that major developmental events, although regulated by binary switches, need not be conserved in evolution. Much as the variability in sex determination weakens the notion of developmental genetic rigidity, we need to investigate what might happen at the population level, where coexisting genotypes come into competition in the evolutionary contest. We know that many binary switches are involved in development, but how are these events translated into real variation at the population level? This is the next threshold of evolutionary biology that must be crossed by many studies, but at present we have few good windows connecting phenotypic variation in a population to a potentially polymorphic machinery of development.

The developmental framework of compartmentalization switches combined with population-level lability is illustrated beautifully by expression patterns of genes affecting eye spot patterns on the wings of butterflies (Brakefield et al. 1996). Eyespots fool bird predators into expecting the prey to be larger than it really is or expecting it to move opposite to the direction that the prey is actually moving. Such patterns have arisen independently in many lines of butterflies but also in distantly related groups such as fishes. Although eyespots may be common in butterflies, there also is a great deal of variation that corresponds to allelic differences, which are subject to selection. This affords a population the possibility of changing patterns in response to different visual environments.

During the late larval and early pupal stage, a compartmentalization process determines regional specialization in the wings. Eyespot formation in the African satyrine *Bicyclus anynana* can be followed by expression patterns of the *Distalless* (*Dll*) regulatory gene, which is commonly associated with proximodistal expression patterns. The location of the eyespot includes an organizing focus, which can be transplanted to obtain ectopically expressed eyespots elsewhere. Genes that affect eyespot location and quality apparently affect anteroposterior axis formation, the number of foci determining the presence of spots, and eyespot size. This is only a partial list of the potential effects, which have been related to mutants in specific developmental genes. Most interesting is the strong degree of lability of developmental gene expression, which allows seasonal polyphenism to allow wing responses to different situations (i.e., an antipredator eyespot changing to a pattern that matches background leaf litter in the dry season; Figure 4.12). Variation in eye-

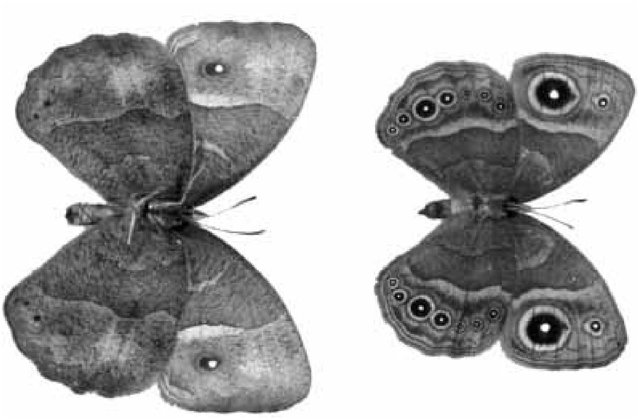


Figure 4.12. Wing patterns of the butterfly *Bicyclus anynana* (**left**) expressed in the dry season when predators are present, selecting for matching the leaf litter background, and (**right**) in the wet season. (Courtesy of Sean Carroll.)

spot patterns appears to be controlled by at least five to six loci and has significantly different patterns of *Dll* expression (Figure 4.13). As in other insects, hormonal control affects factors such as seasonal expression patterns, including wing polyphenism. Thus, *Dll* expression is apparently being modulated to determine either dry-season spotless wings or wet-season wings. The same pathway may have allelic genetic variation that can respond to selection.

Butterfly eyespots tell us something important about the evolution of developmental genes. On the one hand, eyespot expression works within the context of the estab-

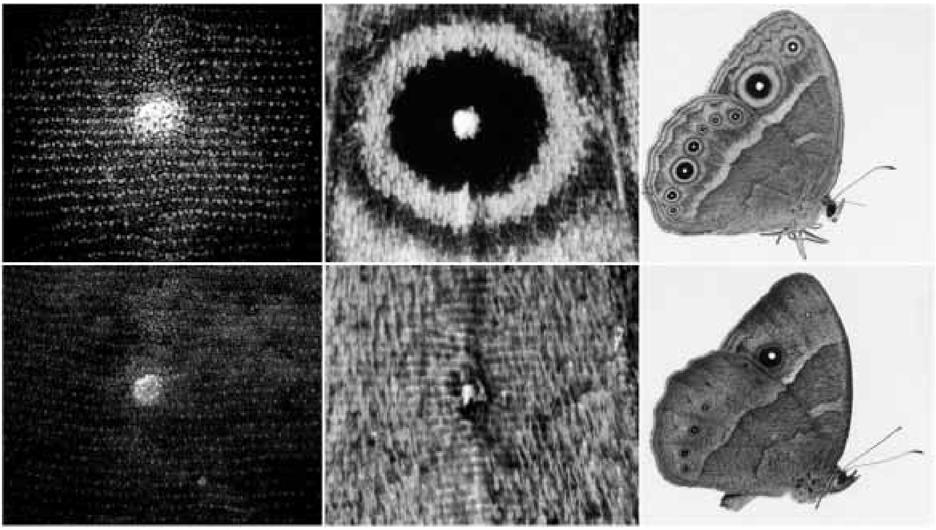


Figure 4.13. Variants in *Dll* expression as correlated with eyespot development in the butterfly *Bicyclus anynana.* The left-to-right horizontal sequences show changes in expression in wing discs from early to later instar larvae, determining large (upper) or small eyespots. (Courtesy of Sean Carroll.)

lishment of lepidopteran wing compartments, where diffusible morphogens or cell–cell signaling molecules determine pattern and location of eyespots. Furthermore, it is possible to isolate genes that determine phenotypic characters such as eyespot size, independent of other factors, such as location or number. But genetic variation and phenotypic plasticity also exist and variation of phenotypic expression in both is of the order of magnitude observed for eyespot presence, size, and character among all the butterflies. This suggests a strong potential for evolutionary lability.

The lability found within butterfly wing patterns can be extended to more distant degrees of relatedness, although not with the specifics of insect compartmentalization. Echinoderms are notable for their development from a bilaterally symmetrical larva to a radially symmetrical adult. It is likely that many aspects of radial development are echinoderm autapomorphies, and developmental gene expression would therefore be of great interest. Lowe and Wray (1997) provide evidence for the recruitment of new developmental roles to functions that were acquired after the divergence of echinoderms and chordates. This can be seen in various genes that have roles in the determination and regionalization of the calcitic endoskeleton, which evolved after the echinoderm–chordate split. The associations of expression with autapomorphic features in the echinoderms represent recruitments of homeobox genes to new developmental roles, although general similarities of gene expression can be traced between echinoderms and chordates, such as the association of *engrailed* with the specification of the nervous system. Lowe and Wray's studies are summarized in Figure 4.14, which shows extensive co-opting of developmental genes to new roles in echinoderm developmental determination.

The apparent recruitment of genes to perform new functions can also be applied to specific evolutionary changes in early echinoderm development. Wray and Raff (1990) investigated the origin of the direct-developing short-distance larva of the urchin *Heliocidaris erythrogramma,* which is derived from an ancestor, *H. tuberculata,* with a planktonic long-distance larva. The evolutionary change ostensibly is focused on changes in the larval stage, where the egg evolves to be more yolky, which fuels a short-distance nonfeeding dispersal stage (Figure 4.15). The ancestral larval state involves a far more complex morphology, required for feeding and moving in the plankton. But the consequences of reduction of feeding/locomotory structures involves a broad suite of changes, including fundamental rearrangements of the timing of gene expression and of major changes in cell lineages and their founder cells (Lowe and Wray 1997; Wray 1992). Nevertheless, the final metamorphosed juvenile is essentially identical, despite major rearrangements of cell lineages and timing (Figure 4.16). Cell lineage histories that do not change can be readily related to larval functional morphology. The loss of the planktotrophic larval stage has occurred with many quite different morphological changes, suggesting that the developmental program is not a rigid cascade, at least in the breakup of the indirect-developing syndrome.

The overall message is clear. Although there is strong evidence for developmental gene determination of compartmentalization and regionalization in development, opportunities for evolutionary change abound by means of allelic variation

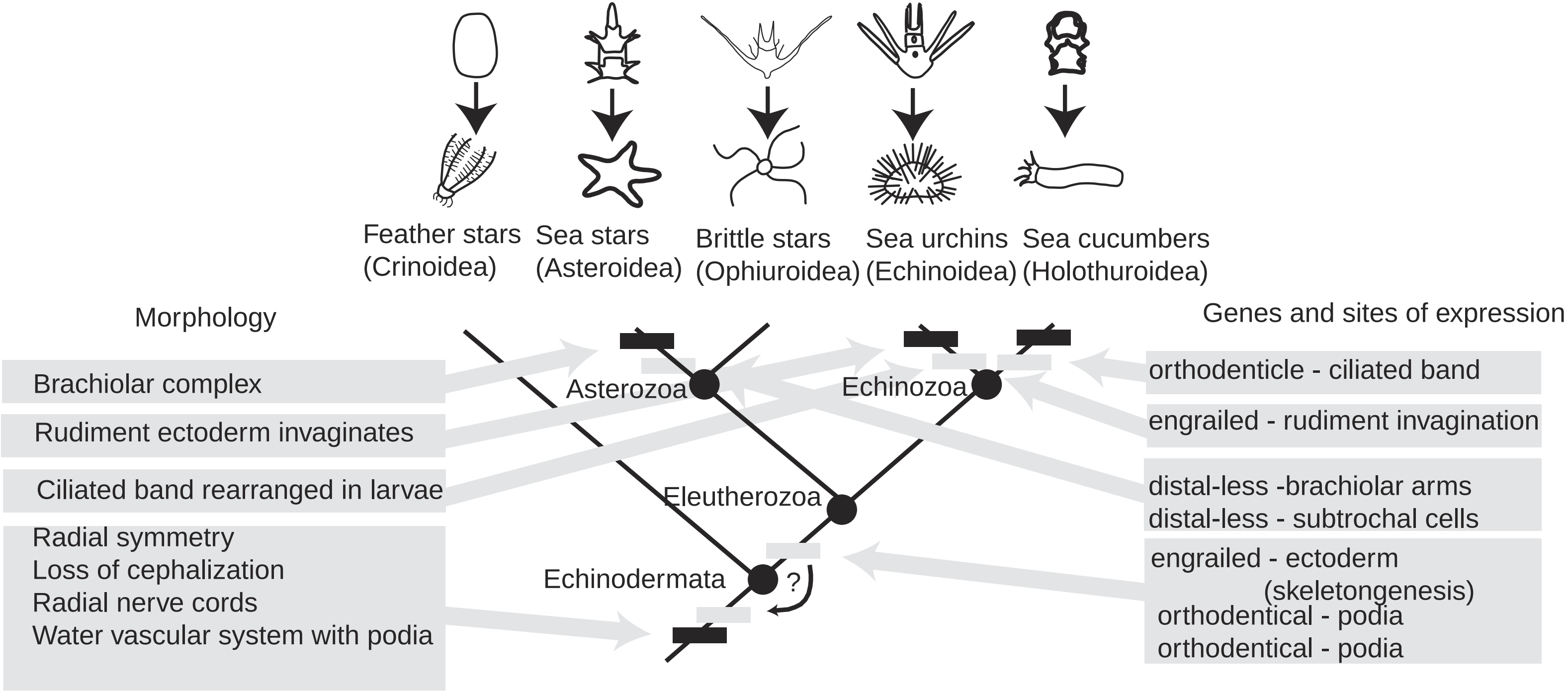


Figure 4.14. Evolutionary history and recruitment of function of developmental roles within the phylum Echinodermata. Reconstructed changes in morphology on left and expression of developmental genes on right. (From Lowe and Wray 1997; reprinted with permission from *Nature,* © 1997, Macmillan Magazines, Ltd.).

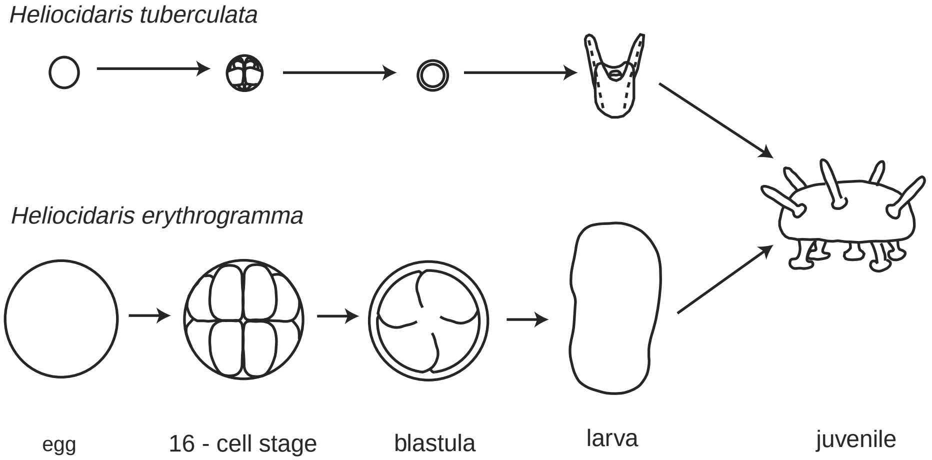


Figure 4.15. Stages of development of the indirect developing urchin *Heliocidaris tuberculata* and its direct-developing descendant *H. erythrogramma.* (After Wray and Raff 1990.)

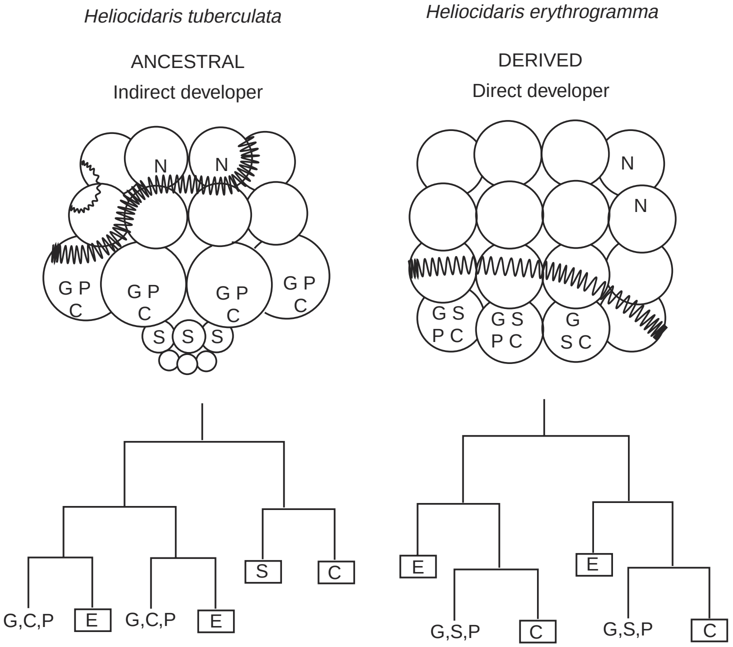


Figure 4.16. Differences in cell lineages between *Heliocidaris tuberculata* and its apparent descendant *H. erythrogramma.* Note differences in fate maps of cell types in above diagrams and differences in lineage maps of eight-cell blastomeres in diagrams below. Wavy line indicates ciliated band. C = coelom; E = ectoderm; G = gut; N = neuron; P = pigment cells; S = skeletogenic cells. (After Wray and Raff 1990.)

within populations, which allows responses to selection of developmental expression (Brakefield et al. 1996) and apparent co-opting of developmental genes to developmentally novel functions (Lowe and Wray 1997). These results propagate an enormous crack in the wall of conservatism in development argued by some and further suggest that the origin of the action of developmental genes in the first place may have been not especially revolutionary but instead incremental in effect.

Limits to the autonomy of developmental fields. For an evolutionary event (mutation) to affect one unit independently of others, the effects of a gene, or set of genes, must be mainly targeted at the most genetically upstream location of determination of the developmental unit. In the case of insect compartments, this is plausible, especially when the few cells giving rise to the eventual polyclone are first instructed. A mutant whose effect is specific to that time and locality might affect the fate of the entire compartment. Subsequent mutations could affect only parts of the compartment under consideration. The same could be said for more vaguely defined developmental fields, such as dental correlation fields.

The autonomy of developmental regions may be limited, which would restrict the shuffling of developmental sequences in evolution. First, the pleiotropic action of mutants may cause widespread effects on the phenotype and not on just a single developmental field. Furthermore, many organisms do not consist of autonomous groups of cells whose spatial interactions are preserved throughout development, after a singular determination of differentiative fate at some crucial point. In vertebrates and other organisms, cell migrations bring groups of cells with previously determined fates into contact. Thus, mutants causing transdeterminations of fate in one group of cells will result in disharmonious functional interactions with other cells with which they come into contact.

In vertebrates, cell mingling and migration in early development is far more important than in insects, which is illustrated by following clones of cells in mouse chimeras. The development of the neural crest in the chick is an excellent example of such complex rearrangement of the positions of embryonic cells (Le Douarin 1980). The neural crest is a transitory structure of the vertebrate embryo arising from the lateral ridges of the nervous primordium. It gives rise to neurons, supporting cells of the peripheral nervous system, and other tissues. During development, cells leave the crest and migrate through the developing embryo, using specific adhesion signals from other cells. The pathways of travel are crucial to the final location and fate of the cells. Even the expression of homeotic mutant systems, such as the bithorax complex in *Drosophila,* can be spatially complex. A group of more than 20 genes control the spatial morphological expression of bithorax genes (Jurgens 1985).

To the degree that such intricate migration or spatially complex genetic expression occurs, the probability diminishes that independent developmental units can be transdetermined completely into functioning new units. After all, it may be possible to change the fate of a migrating cell from the neural crest, but it will find itself in a localized region "designed" to accommodate another neurological structure. Thus, the degree of cell migration increases the probability that disharmonious interactions will result in a phenotype of low viability.

Morphological Gradients, Units, and Discontinuities

Positional signaling and pattern formation. Proper development depends on mechanisms that translate signals into spatially significant responses. Major patterns, such as segmentation in insects, are established very early in development. The question is how a group of cells "interprets" their position to produce a series of structures that are spatially correct (Wolpert 1969). It has been generally thought that some mechanism of positional signaling is necessary to generate spatial inhomogeneity across a group of cells. Individual cells would then be induced by interpreting their position either at a specific stimulus level in a spatial gradient or by their location (Figure 4.17) at a local peak of stimulus (Stern 1968, pp. 136, 159). Three principal mechanisms of inhomogeneity have been proposed: (1) concentration gradients of morphogens; (2) mechanochemical stimuli producing waves through chains of cells; and (3) electrochemical fields. Most suggestions either are based on the presence of spatial inhomogeneities, as in electrochemical differences across cells (Nuccitelli 1983), or stem from plausible models, as in the cases of mechanochemical approaches (Oster et al. 1983) or diffusion of morphogens (Meinhardt and Gierer 1974). For illustration, I will show how spatial inhomogeneities might be generated and interpreted with the morphogen and mechanochemical models. We have discussed above a model for gastrulation using mechanochemical interactions in a sheet of epithelial cells (Odell et al. 1981).

Morphogens might be complex molecules or simple inorganic constituents; we require only that they can be established in a spatial gradient. These would depend on either diffusion or active transport across groups of cells. At the time of determination of spatial arrangement, most primordial structures are about 100 cells or fewer in size (Wolpert 1969). Given a simple diffusion model and given the known developmental period of several hours, a morphogen diffusion gradient can operate over a field of cells of a few millimeters (Crick 1970). A series of *diffusion-reaction* models have been suggested in which cells at local peaks or thresholds of morphogen concentration react by developing in a specific fashion (Meinhardt and Gierer 1974; Turing 1952). The cells are said to contain a *prepattern,* which determines the fate of the cells depending on the local morphogen concentration. In par-

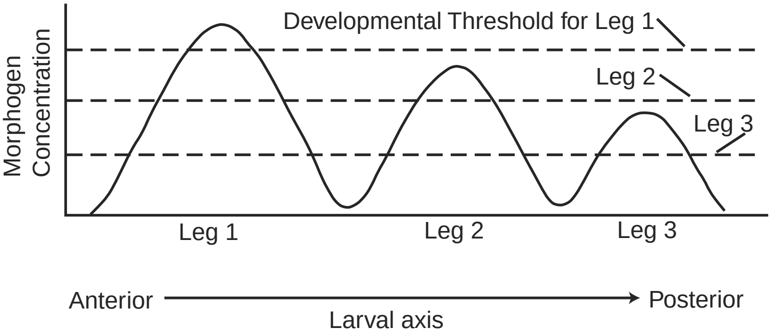


Figure 4.17. The development of a structure may be initiated above a threshold, within a concentration gradient of morphogen. (After Stern 1968.)

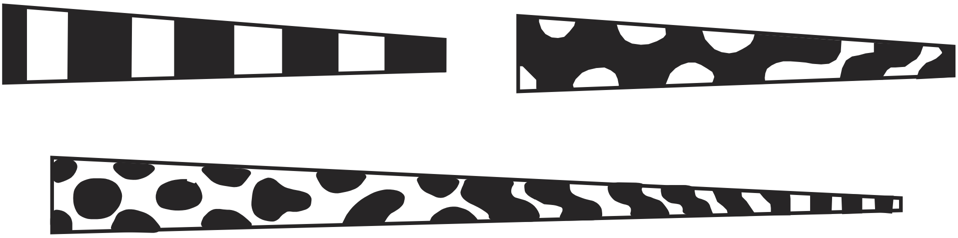


Figure 4.18. Generation of different tail color patterns by a diffusion-reaction model. (From Murray 1981, with permission.)

ticular, Murray (1981) modeled coat color in mammals by assuming that two substances with different diffusion coefficients diffuse and react on a two-dimensional surface. The size and shape of the primordial field (set up in the embryo) is crucial in the determination of pattern, as this determines how diffusion and local reaction can permit given concentrations to develop at any given spot in the developmental field. In a tapering tail, for example, an increase in size changes the determined pattern from striped to dappled (Figure 4.18). This variation seems to fit the known range of patterns in felids. Murray also successfully modeled scapellary stripe markings in zebras. The patterns are constrained by the presumed diffusion mechanism, which works in the embryo (Figure 4.19).

Peaks in concentration can be generated from simple cell-to-cell diffusion by the creation of minor local instabilities (Turing 1952). An analogy can be drawn with an electrical oscillator, whose frequency is determined by its characteristics. The oscillations will be initiated, however, by random disturbances in the circuit. The phase, but not the wave length or amplitude, will be determined by the timing of the disturbance. The latter two parameters are determined by the number of reactants, the dif-

Figure 4.19. Coat pigment pattern of an adult tapir. It is likely that this stark color pattern was established by a diffusion-reaction field in the embryonic ectoderm. (Photo by the author.)

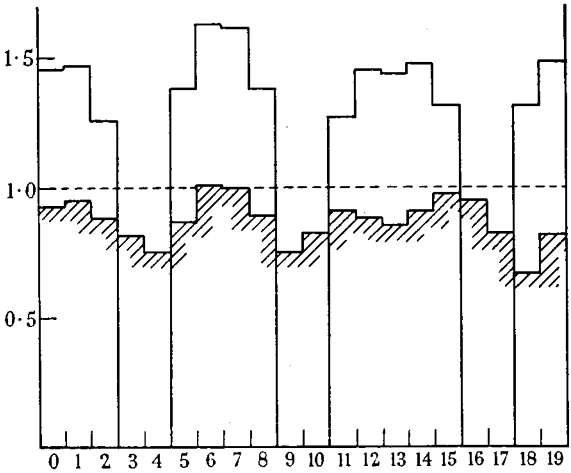


Figure 4.20. Development of spatial inhomogeneity (clear bars) following a local perturbation in concentration of a diffusible substance (hatched bars). (Details of model in Turing 1952.)

fusion coefficient, and the fluid through which diffusion occurs. With a small disturbance (i.e., a departure from a previous equilibrium), diffusion from one cell to another will commence, resulting in a chain reaction and a potentially long-term spatially cyclic variation in concentration. In a ring of cells, the interactions of two or three morphogens are sufficient to form regularly spaced peaks (Figure 4.20) of concentration, given some initial local instability in the ring (Turing 1952). Simultaneous spread of an activator and an inhibitor of morphogenesis can result in spatially regular peaks with random fluctuations of activator concentrations at the source of activator production (Meinhardt and Gierer 1974). Local instability, such as a contraction event of the apical end of a cell, can also generate waves of movement through adjacent cells (e.g., Oster et al. 1983). Here, too, other parameters (e.g., elastic properties of cells, rates of reaction to chemical stimuli) would determine the wave length and amplitude of response.

Such models require that local cells interpret correctly simply the presence, concentration thresholds or relative concentrations of a morphogen concentration, or the presence of some other ligand. During the 1990s a vast array of examples have emerged to verify the presence of signals that had been hypothesized for decades, especially cell communication factors (e.g., *hedgehog* and *wingless* in *Drosophila*), that are the agents of communication in (usually) early developmental fields. Diffusible morphogens such as retinoic acid interact with other factors to switch on spatially localized batteries of genes that eventually yield segments, limbs, and digits. On a spatial scale larger than diffusion, color pattern in the Himalayan rabbit seems determined by threshold reactions of local cells to temperature. There is a variant of the Himalayan rabbit that has variable pigmentation, depending on ambient temperature (Iljin 1927; Sturtevant 1913). A variable prepattern throughout the body interacts with a threshold temperature. At high ambient temperatures, the rabbit is all white, whereas at very low temperatures, the animal develops uniformly dark

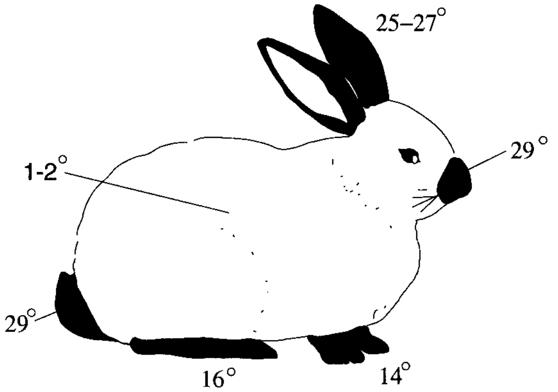


Figure 4.21. Himalayan rabbit raised at a temperature below 14°F. Temperatures listed represent critical body surface temperatures, above which no pigment is formed. (After Stern 1968.)

coloration. At intermediate temperatures (Figure 4.21), poor blood supply to the extremities causes the skin to drop below a threshold temperature, resulting in the deposition of melanin. The remainder of the rabbit is pale.

Whatever their cause, gradients across primordia are important in the determination of development. The chick limb bud, a primordial structure that elaborates the limb, is one of the best studied systems indicating the presence of such gradients. A mesodermal structure induces the formation of the *apical epidermal ridge* (AER). Soon after, the rest of the ectoderm loses the ability to form AER. A maintenance factor produced by mesoblasts just below the AER is required to maintain its activity. Excision of the posterior part of the AER causes many abnormalities to develop in the limb, but excision of the anterior part of the AER causes few abnormalities, save the elimination of anterior structures (Hinchliffe and Gumpel-Pinot 1981). If a posterior part from another embryo is implanted in the anterior part of another chick, the second chick will develop the mirror-image digit pattern (anterior to posterior: 432234). Such experiments lead to the inference that a zone of polarizing activity exists in the bud posterior, and that a morphogen diffuses anteriorly. Implants at different distances suggest that the field of reaction is about 300 micrometers long (Summerbell 1981). Dorsoventral and proximodistal concentration gradients are also required to provide sufficient information to form the limb (Meinhardt 1983). It is not clear whether formation of digits is induced at concentration peaks, or whether thresholds of concentration are involved. Higher cell growth rates in the ZPA may result in the posteroanterior gradient of the morphogen retinoic acid (Duboule 1994). As it is known that very different mechanisms occur, for example, in the formation of interdigital spaces in reptiles (differential cell proliferation) versus amphibians (interdigital cell death), we should expect spatial developmental mechanisms to vary among taxa.

As discussed above, anteroposterior and interparasegmental gradients in fruit flies are set up by gene products set in motion by the action of *Hox-C* genes. Some of these interactions are known to involve diffusible morphogens. In the milkweed bug *Oncopeltus,* the chain of segments sets up something analogous to a wave pattern; structures within segments are determined by the phase in relation to other elements. The segmental gradient in two successive segments can be likened to a gradient of values (10, 9, ... 2, 1, 0/10, 9, ... 2, 1, 0). Experimental apposition of values 2 and 8 results in the intercalation of positions 1, 0, 10, 9. If positions 5 and 5 are opposed, no intercalation occurs (Lawrence 1981). In insects, some of the anteroposterior difference in cuticular structure may be due to anteroposteriorly oriented basal cytoskeletal extensions, or feet, which contract and cause transverse ripples (Locke and Huie 1981). The initiation, extension, and contraction of the feet may be hormonally controlled, perhaps by ecdysteroid in the hemolymph.

Evolution of discontinuous traits. The quantum nature of pattern determination raises two important points for development and evolution. First, variation in morphogen concentration, or number of concentration peaks in a field, may have an important effect on the phenotype. Second, the evolution of increasing and decreasing numbers of units may involve crossing and readjustment of thresholds to prevent the formation of partial structures. Developmental programs are usually evolved to generate complete, rather than partial, units. This suggests the action of strong stabilizing selection on morphogen concentration gradients during pattern formation. Such stabilizing selection acts to control the expression of many genes in combination, to effect a series

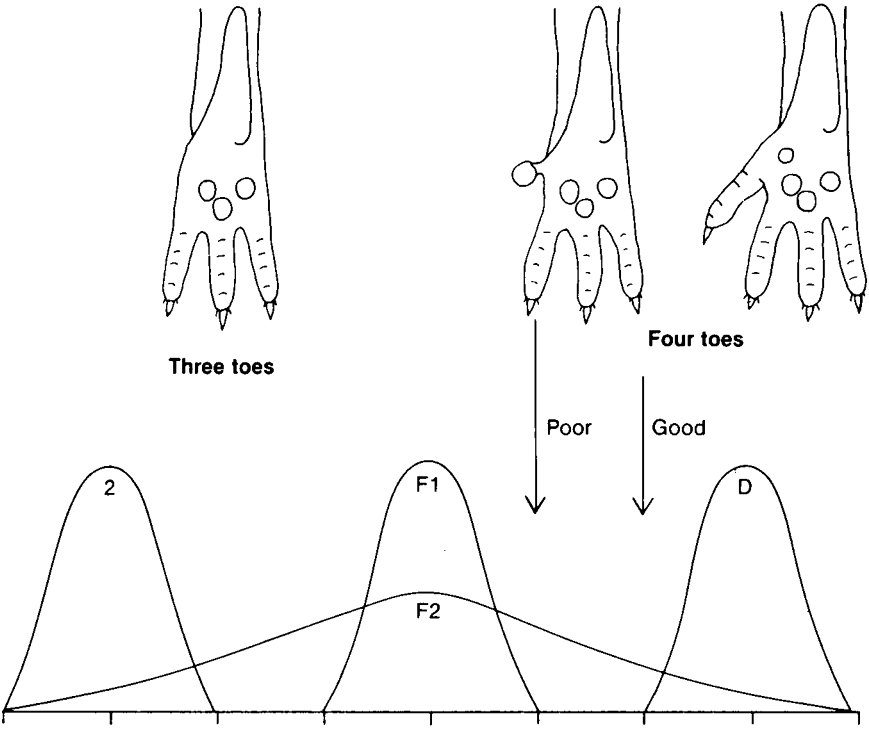


Figure 4.22. Genetic control of toe number in guinea pigs. Arrows refer to thresholds for poor and good development of four toes. A cross of strains "2" and "D" results in an F1 generation with individuals all beyond the threshold determining three digits. Segregation in the F2, however, results in an expansion of genetic variability, across the threshold required for four-digit morphs to reappear. (Adapted from Raff and Kaufman 1983.)

of discrete phenotypes, such as complete toes (Figure 4.22). The discrete phenotypes are expressed, despite some genic variation and despite environmental variation.

To understand the problems caused by natural variation in developmental gradients, let us consider a simple field of length *S,* with a series of sinusoidal waves of morphogen concentration, with wavelength *L.* Assume that no partial structures are formed and that the number of repeated structures corresponds to the integer nearest to *S/L.* Variation in *S/L* should be the outcome of variation of flux of morphogens, size of the field, and variation in the reacting cells. How much variation in a developmental signal can occur before it is no longer possible to permit the vast majority of individuals to develop the appropriate number of segments or digits?

If variation of other traits is any clue, the coefficient of variation of either *S* or *L* is likely to be no less than 2% or 3%. This sets a limit on the organism's probability of producing the correct number of repeated structures (Maynard Smith 1960). Above a repeat number of 5 to 7, natural variation precludes the possibility of getting it right, at least more than 95% of the time. For example, to produce the exact number 30 in over 95% of the population, the coefficient of variation of *S/L* must be less than 0.85.

This consideration provides a mechanism for a common observation that quantal structures vary from the mode more often in large repeats than in small repeats. We often relate this to the functional importance of producing an exact small number of structures – heads or digits, for example – as opposed to an inexact larger number of units, such as hairs. The difference in determination may, however, be due to a developmental constraint combined with natural variation.

There are cases in which numbers of units vastly greater than 5 to 7 are determined exactly. Segment number in leeches is fixed at 33. Regeneration experiments in some polychaete annelids suggest that when a few segments are removed, the regenerative process reestablishes the correct number. This suggests that more than a simple overall diffusion-reaction mechanism operates to ensure an exact number of repeats. Segmentation in annelids and insects seems often to include patterns involving interactions within segment pairs (e.g. Nüsslein-Volhard and Wieschaus 1980); this can give more localized control on segment number.

An appropriate genetic model regulating the determination of complete units would incorporate stabilizing selection on developmental mechanisms. Concentrations typically falling near a threshold between the determination of different structures would often cause serious errors in development. One would expect, in a population with modal digit number *n,* a distribution of effects, with the mode centered farthest away from any thresholds (Lande 1978; see chapter 3). Genotypes would be expressed as different phenotypes depending on their respective relationships to the physiological threshold (Figure 4.23). This would ensure that any small genetic variation from the mode would still result in production of the appropriate phenotype.

Consider selection from *n* to *n*-1 digits. This must have occurred in lizards such as those of the genus *Bachia,* in which digit reduction is associated with the evolution of the fossorial habit. As selection proceeds for reduced digit number, the mode of genetic variants will be shifted to a predominance of genotypes near a threshold of determination between *n* and *n*-1 digits. Near this threshold, we would expect that incomplete units will be more common in the population, along with phenotypes with

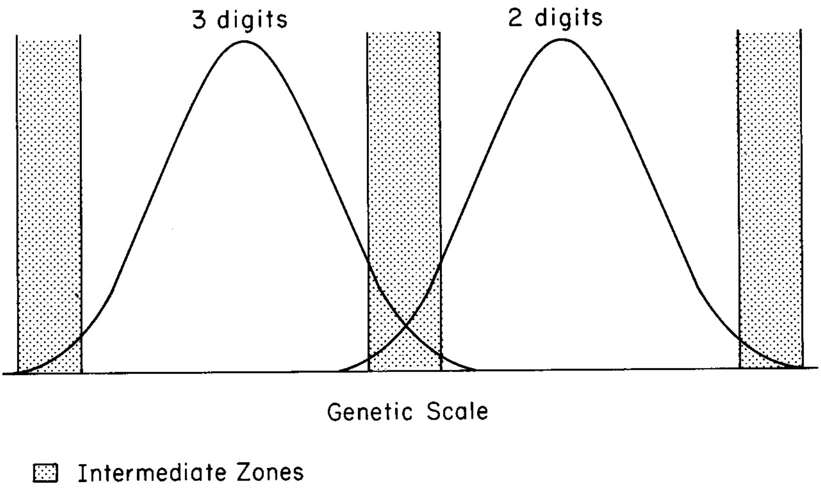


Figure 4.23. Model of polygenic digit determination in lizards with threshold effects determining phenotypic expression.

n and n-1 units. Incomplete units, such as segments and vertebrate skeletal articulations, can be common in natural populations (e.g., Wells 1957; Williams 1950), but we presume that there is usually selection against such incomplete determinations.

During the evolution of digit loss, one should expect a difference in phenotypic evolutionary rate. At first, the center of the genotypic frequency distribution will be centered on those genotypes determining n digits, and far from the threshold for n-1 digits. Selection at this stage cannot be a very powerful process owing to the low diversity of phenotypes. But when the distribution shifts such that the mode is near the threshold, deviant phenotypes are more frequent and selection will work more rapidly. If we assume a normal distribution of effects along a phenotypic scale, with the mode centered between the thresholds (Figure 4.23), the rate of change should be proportional to $x\ h^2s$, where x is the position on the genetic scale, h^2 is the heritability, and s is the selection coefficient. When the distribution is centered on the threshold, the rate is proportional to 0.395 h^2. The rate of change is approximately six times faster when the center of the distribution is farthest from the threshold (Lande 1978). This provides a mechanism for rapid transition from one digit number to another. Using a conservative value of 0.1 for h^2 and 0.01 for s, change could be effected in 29,000 years. A normal selection model, combined with a threshold model of determination, can therefore effect rapid transitional evolution between dominance by different discrete phenotypes.

The evolution of unit number must be intimately involved with the determination of thresholds. How does the presence of thresholds influence the rate and pattern of change of a system regulated by pattern formation? This has long been a subject of great interest. Goldschmidt (1938) discussed the phenomenon of phenocopies or environmentally induced variant phenotypes that resemble major mutant phenotypes. These variants are usually induced by either heat or cold shocks. Although the majority of the variant phenotypes are not genetically transmissible, a small proportion of the variation has a genetic basis.

Waddington (1956) demonstrated that artificial selection for phenocopies can produce strongly discontinuous changes in laboratory populations. Using temperature shock, he induced a phenocopy of *cross-veinless,* a mutant with a strongly altered wing. Artificial selection for the phenocopies resulted eventually in flies that developed *cross-veinless* wings in the absence of the temperature shock. A similar experimental design produced phenotypes with metathorax partially converted into mesothorax (Waddington 1956). This change, termed *genetic assimilation,* can be explained by the cumulative action of many genes moving developmental determination past a threshold. The developmental "defect" is now no defect at all, as selection has produced a harmonious combination of genes producing a deviant phenotype.

Evolution in most situations will not involve induction of such phenocopies. Furthermore, natural selection should not be expected to necessarily favor the phenocopies, even if they are being induced by a sudden environmental change. The phenomenon of genetic assimilation, however, indicates that previously available and genetically controlled developmental programs can be mobilized and perhaps favored by natural selection.

At the level of embryogenesis, these discrete jumps suggest the presence of prepatterns that can be induced to determine new and discrete phenotypes in the population. Sohndi (1962) performed a selection experiment on a laboratory *Drosophila subobscura* population with predominance of the *ocelli-less* mutant, which lacks ocelli and bristles on top of the head. After 40 generations, there was a noticeable increase of response. At that time, females had essentially the wild-type configuration of ocelli and macrochaetes. With further selection, neomorph setae arose between orbital and ocellar setae, a pattern never found in the Drosophilidae but typical of the Aulacogastridae. Selection may have involved decreasing amounts of a precursor that first determined the *ocelliless* phenotype, then the wild type, and finally the wild type plus neomorph arrangement. The wild-type cells in normal population may therefore have the prepattern but may not be able to produce the new phenotype, owing to a lack of sufficient morphogen.

These threshold effects should be distinguished from major developmental reorganization. The thresholds have already been built into the determination of the phenotype to ensure proper development, though some may have been suppressed during evolution. Natural selection works within the available developmental constraints. All the variation has been evolved and exists currently. The pattern of character appearance is nevertheless saltatory. Such saltatory changes can occur as a matter of normal selection processes and need not require major genetic reorganizations or speciation.

Development, Genes, and Selection: The Evolutionary Ratchet

The developmentalist point of view presented above leads to a model, which I call the *evolutionary ratchet,* generating some of the constraints in evolution. The model characterizes an organism as being a product of a long evolutionary history, where the evolution of timing, rates, and localization leads to a complex developmental process that can be disrupted less and less easily as time progresses. Any spatiotemporal interactions in the developing phenotype that, when accumulated, cannot be disrupted because of integration are accumulated by the *epigenetic ratchet* and lead to *epigenetic constraints* (see Rachootin and Thomson 1981). Shifts in tissue interactions are well known in evolution (Hall 1984), but such transitions may be difficult to achieve owing to interdependencies between different germ layers. Riedl (1978) thought of changes in developmental patterns of such complex organisms as carrying a high *burden.* "By burden I mean the responsibility, carried by a feature or decision. ... With systemization (i.e., the evolution of development) the functional burden carried by decisions increases and with this a new lack of freedom called canalization also increases" (Riedl 1978, p. 80). He argued that "patterns of decisions that have a certain degree of burden have no real prospect of being fully dismantled" (p. 93). Mechanistically, canalization must involve a narrowing of phenotypic expression, despite a range of genotypes affecting the trait (Figure 4.24). Selection must favor a reduction of plasticity, even in the face of some genetic variability.

Two more factors contribute to the overall evolutionary ratchet. The *genetic ratchet* refers to new genes that, when incorporated, cannot easily be lost by processes such as genetic drift. Pleiotropy is one likely explanation. Incorporated genes having widespread effects on the overall phenotype may not be easily lost in evolution (Kollar and Fisher 1980; Lande 1978). Many *cis*-acting enhancer sequences are now being discovered that regulate expression of genes hundreds of base pairs away. For example, a 125-base-pair DNA segment regulates expression of the yolk protein 1 gene of *Drosophila melanogaster* (Garabedian, Shepherd, and Wensink 1986). This enhancer-structural gene complex may be stabilized by this positional arrangement, especially if the enhancer is required for expression of other nearby genes.

Ohno (1973) characterized other modes of incorporation by the genetic ratchet as "frozen accidents." Accumulation of deleterious mutants in chromosomes with low recombination and dosage compensation in the X chromosomes of mammals are examples. Evolution after the development of dosage compensation (inactivation of one of the two X chromosomes in the female) would select against translocations of X-linked genes to other chromosomes. The X chromosome seems to always be about 5% of the total mammalian genome.

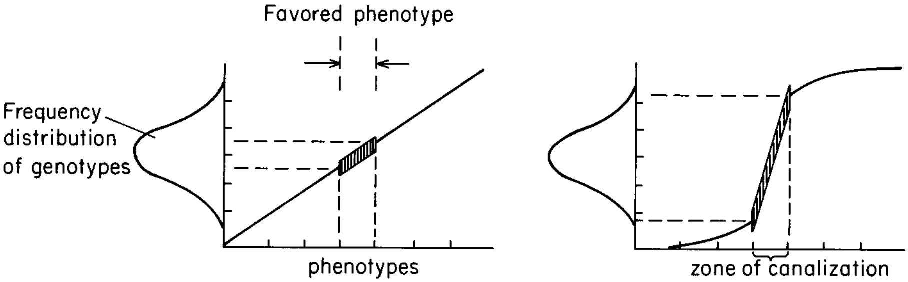


Figure 4.24. Canalization of a trait, showing reduced phenotypic expression, despite genetic variability that might cause more variation in phenotypic expression.

Such a model is evocative of the reverse of the adaptive landscape metaphor of topographic peaks, connoting high fitness. Instead, evolution cuts channels, forming the developmental landscape. Waddington's *epigenetic landscape* was conceived as a reflection of the limited number of stable developmental pathways possible from the combined actions of different genes involved in development. "The reactions of these genes with one another (and with the environment) interlock so as to define a developmental track which will always be followed by the antennae of flies of a certain genotype. . . . The normal developmental track is one towards which a developing system tends to return after disturbance" (Waddington 1940, p. 93). The pictorial representation of this is the steepness of the walls of the valleys, which reflect the tendency to return to the developmental track if a deviation from the central stream occurs. Such a theory acknowledges that the evolution of internal organization is as important as the effects of the external environment. As Riedl (1978) put it: "Selection does not work from the outside only" (p. 244).

The *selection ratchet* refers to features that once acquired, are not easily lost, owing to functional integration within the developing phenotype. For example, the presence of the vertebrate humerus is essential in the function of the radius and ulna. On functional grounds alone, the humerus should be the last structure to disappear as limbs are reduced in evolution. In the construction of functional morphological models, all three types of constraints – epigenetic, genetic, and selectional – will have to be incorporated into the study of morphology and adaptation.

The evolutionary ratchets complement neo-Darwinian theory; we only acknowledge that evolution tends to organize the phenotype and genotype so that it begins to resist some directions of evolutionary change for reasons of internal organization. Such presumptions are implicit in the works of the founders of the Modern Synthesis (e.g., Dobzhansky 1970; Mayr 1963; Stebbins 1950), although genetic, rather than epigenetic, interactions have been emphasized. Maderson et al. (1982) take such points about development and evolution to be major challenges to the Modern Synthesis. They are not. As Riedl (1978, p. 235) noted: "In terms of feedback it is a selectional theory. It assumes the correctness of the Neodarwinian synthesis as a precondition, but supplements this." The concern for constraints influences our conception of the mechanisms that regulate the nature of variation, but neo-Darwinian theory focuses on the fate of variation, once it is generated. There is therefore no conflict at all between the two approaches; they are complementary.

Evolution and internalization of developmental programs: phenotypic integration. Parts of an organism do not evolve function, nor are they genetically determined independently of the rest of the phenotype. The entire body – and certainly large parts of the body – consists of tightly integrated biological units, from the points of view of genetic determination, development, and function. This fact is acknowledged implicitly when evolutionary biologists view the phenotype as a unit of selection, and not individual genes, developmental tracks, or parts of the body. It is fitness that matters, and fitness is determined by the functioning of the entire phenotype.

The postulation of an evolutionary ratchet begs the question of how developmental, genetic, and functional integration correspond in a living organism. On the level of phenotypic variation, one might ask whether phenotypic correlations among functionally related traits are strong. The same question might be asked of developmental and genetic correlations. If functionally related traits are strongly correlated genetically, then evolution will operate on blocks of the phenotype that have functional significance. A correspondence between genetic correlations and functional relatedness of traits might suggest that the genotype is a coevolved unit, designed to serve the entire organism. This concept has been advocated strongly by holistic geneticists such as Ernst Mayr (1976).

It would be of great value to describe the relationships between phenotypic correlation and degrees of functional, developmental, and genetic integration (Olson and Miller 1958). Unfortunately, detailed studies are few and incomplete. A study of the cranium of rhesus macaque suggests that such a correspondence may not exist, or is at least more complex than we can uncover (Cheverud 1982). Although functionally related traits are relatively tightly integrated, genetic correlations among the traits can have a completely different pattern. These correlations may arise through stochastic processes, suggesting that the integration of the phenotype is maintained by a continual process of natural selection. Cheverud noted that some of the genetic correlations do correspond to expectations of functional integration and may reflect the action of stabilizing selection along ridges or on peaks of the adaptive landscape. The nonadaptive genetic correlations provide opportunities for new directions of evolution.

The three ratchets determine the difficulty of losing a gene or phenotype at the present time, but the current situation does not indicate how the traits or genes might have evolved. As this process continues, order becomes important and internal relationships become as important as interactions with the external environment. If the program is organized as a unit, it may then become internalized; that is, a genetic-epigenetic mechanism seals it off from the external environment, allowing it to interact and evolve dependencies with other such units. Once such units evolve, internal constraints will direct evolution and the units may be shuffled as organized entities with other such units. Evolution would no longer consist of infinite molding by the external milieu, as might have happened during the evolutionary building of a given unit. A fundamental problem in the evolution of development is to understand whether such internalizations produce fixations of form that can no longer be changed, even with the aid of natural selection. As developmental programs evolve, form could conceivably become channeled to a degree that there is no variation on which natural selection could act. This would be reinforced by redundancy in developmental systems that rescue mutants that might cause variation in form. The four sets of duplicated *Hox-C* genes in vertebrates could be envisioned as such a redundant system (McGinnis and Krumlauf 1992).

A possible example of the combined action of the genetic and selective ratchets is the sequence of incorporations of evolutionary changes underlying a functioning protein. Tryptophan synthetase A is an enzyme of 267 amino acids in the bacterium *Escherichia coli* (Allen and Yanofsky 1963). At position 210, a substitution of serine for glycine (the wild type) causes no change of activity. A mutant with glutamic acid at this site eliminates function. If, however, this nonfunctioning mutant encumbers a further change, of tyrosine to cystine at site 174, full function is restored. The same change, at site 174, of the wild type protein eliminates function. Thus, the same mutant (tyr→cys at site 174) will destroy or save the phenotype's full function, depending on the order of incorporation. The sequential incorporation of mutants, moreover, may result in a frozen ensemble of changes that cannot be removed except by rare double mutants. The phenotypic and genotypic basis of a functioning phenotype is therefore as much a matter of the order of genetic incorporation of change as it is a matter of function per se.

One might apply these ideas to a theory of reduction of plasticity over long periods of geological time. Valentine (1969) noted that phylum-level origins were confined to the early history of the Metazoa. A combination of restricted ecological, genetic, and developmental opportunities may now preclude the origin of many new phyla. Jaanusson (1985) described the decline of variation through the Paleozoic in segment number among species of trilobite families, and the importance of commitment caused by the rise of functionally integrated structures. Living forms may be more constrained than those that were present at the dawn of the Metazoa.

Critique of the ratchet theory

Developmental gene specification: the music allows many styles. The conservation of sequence and position of genes across a wide span of phylogenetic landscape suggests that a functioning developmental gene set has maintained its integrity over hundreds of millions of years. The genetic and developmental ratchet models explain this apparent constancy as a pattern of development whose disruption would result in severe losses of fitness. We cannot be sure, however, that it is locked into place. It is possible that the members of the *Hox* gene family and other developmental genes can be better likened to a music score, where the notes might be the same, but the arrangements and timings might be varied from organism to organism and from function to function. One animal group might be Rock and Roll, another Beethoven, but both can be read from a score with the same notes and timings.

Lability of developmental programs. The notion of hardening of developmental programs has been seen by many as a fundamental challenge to the notion that natural selection is unrestricted in its bounds. The evolution of development is thought by many to bias evolutionary direction (Alberch 1981, 1982; Davenport 1979; Gould 1982b; Maderson et al. 1982). These arguments, furthermore, point to the creative power of combining units that are relatively independent to produce novel structures (e.g., Løvtrup 1974). For example, the rise of the *Hox* animal gene complement has been considered to be the great event of animal evolution, permitting a Cambrian explosion of life (Valentine et al. 1996). Minor changes in temporal arrangement of developmental timing would be the cause of large macroevolutionary jumps (Gould 1982b). Differences between major baupläne, moreover, would be ascribed to differences in embryogenesis that may have arisen by accident or for reasons of internal organization, and not selection to function in the external environment. This reasoning is premature and may lead us too far in the opposite direction. As discussed above, the nature of *Hox* action is clear and conserved, but the many variations in expression pattern call into question any rigidity of evolution or to suggest any revolution in genetic control.

Restrictions of evolutionary change may well be true at some levels of development. But different developmental pathways might lead to the same overall adult phenotype, which may have been selected to function optimally in the environment. In these systems, the burden of developmental restriction may be relatively unimportant. Frogs are notable for their overall adult morphological homogeneity, despite great antiquity and among-species genetic distances, relative to other groups such as mammals (Cherry, Case, and Wilson 1978). Is this adult homogeneity determined by a singular developmental ground plan that has been hardened to the extent that no fundamental change is possible? Apparently not. Early development in the hylid frog genus *Gastrotheca* is quite different from that of other frogs, yet the adult form looks like a typical frog (del Piño and Elinson 1983). Almost all of the body forms from an embryonic disc, a group of cells that forms from fusing cells of the blastoporal lips. In two other unrelated genera, similarly located yolk-poor cells are spread around the blastopore, instead of being concentrated in a disc (Figure 4.25). The difference in *Gastrotheca* development is due to a temporal separation of the times of closing of the blastopore and the anterior extension of the archenteron. The embryo of *Gastrotheca* looks birdlike or reptilelike as it initially develops into several sheets of tissue, which secondarily form tubes after folding. This disk, however, is formed by gastrulation and is not homologous with those of other vertebrates.

The difference in the early development of *Gastrotheca* might be due to extraordinarily slow development (two weeks from fertilization to end of gastrulation, as opposed to one day in *Xenopus laevis*), which results in the temporal separation of the closing of the blastopore, the anterior movement of the archenteron, and fundamentally rearranged tissue interactions, relative to other frog embryos. Slow development is related to an overall syndrome of egg brooding, maternal incubation of embryos, multinucleate embryogenesis, and very large eggs. Some of these have ecological significance; the environment may have selected for the rather unusual parental traits. *Gastrotheca* females lay eggs in water-poor habitats; this simple difference is probably the driving force for the profound larval and developmental differences from other frogs. The novel development of *Gastrotheca* organizes the developing embryo as an elongate disc lying above a large amount of yolk. The alternative development of *Xenopus laevis* and other anurans produces an elongate embryo (Figure 4.25) adapted for early swimming (del Piño and Elinson 1983). But no macromutation changing adult development has occurred; the adult is still basically a frog. As del Piño and Elinson (1983, p. 589) note: "The embryos of *Gastrotheca* illustrate that it is possible to modify greatly the pattern of early development without altering the basic adult morphology." In this case, adult stasis cannot be said to be due to a rigidity of developmental program.

Development in the freshwater clam *Unio* suggests that natural selection can break up seemingly fundamental embryological spatial interactions, yet a typical adult is produced. Its larval stage is highly modified relative to its closest marine relatives. Larvae are brooded until the glochidium stage, which bears a pair of hooked valves capable of attaching to the gills of fishes. It completes development on the gills and eventually drops off to finish development in soft sediments. *Unio* would be expected to have spiral cleavage, a characteristic mode of early cell division common through-

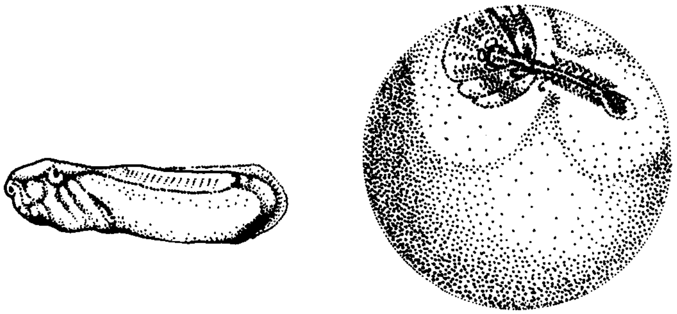


Figure 4.25. Comparison of frog embryos. On the right, *Gastrotheca riobambae* embryo is spread on the yolk, whereas the embryo of *Xenopus laevis* (left) is elongated, showing its adaptedness for early swimming. Bar = 0.5 millimeters. (After del Piño and Elinson 1983.)

out annelids, mollusks, polyclad flatworms, and other related phyla. At the third cell division, typical groups with spiral cleavage show a differentiation between four macromeres and four micromeres. After the next few cell divisions, the spiral arrangement of cells is apparent. The embryo at this stage is mosaic, which means that cells have specific fates that cannot be easily reversed. In most mollusks, the first generation of micromeres divides and forms eight cells, which eventually form the apical region of the embryo and the prototroch, a larval feeding organ. But these structures are lacking in *Unio* larvae, due to a retardation of division in the first tier of micromeres. The second tier of micromeres, arising (as is normal) from cleavages from the macromeres, gives rise to the bulk of the larva. The importance of other micromeres has been greatly exaggerated relative to the typical pattern of spiral trochophore larval development in most related groups (Lillie 1895). This alteration seems related to the development of structures of ecological relevance, such as the powerful adductor muscle used by the larva to hook the valves onto prospective fish gills. As in the amphibian case, major adjustments can be made in early development to satisfy ecological necessities, with little consequence for the subsequent adult phenotype.

Ancient locking of developmental genes? Our discussions above of major developmental genes and gene networks further reinforce the conclusion that developmental programs are not nearly as fixed and immutable as might have been suggested by past notions of the evolution of rigidity in the evolution of ontogenetic programs (e.g., Slack and Holland 1993). The following important points emerge:

1. Variation in the action of Hox genes can now be found as population-level polymorphisms (Brakefield et al. 1996).
2. Seemingly fundamental milestones in the evolution of animals, such as the appearance of a notochord, can be lost in evolution, even as a consequence of rather small-scale changes in life history patterns stimulated by population-level natural selection events (Swalla and Jeffery 1996; Jeffery 1997; Wray and Raff 1990).
3. Genes and gene action involved in crucial patterning of developmental events, ranging from setting of anteroposterior axes at the very start of development to sex determination, are not necessarily found as an identical genetic network throughout large parts of an animal phylogeny (Saccone, et al. 1998; Wimmer et al. 2000).

4. Motifs of gene action and even gene networks are redeployed in different functions at different times and locations during development (Lowe and Wray 1997, Heanue et al. 1999).
5. Major changes in animal body patterning have occurred with no major changes in presence of *Hox* genes (Grenier, et al. 1997).

While it is clear that *Hox* genes are crucial in setting off the cascading actions of developmental genes and that makes their evolution crucial in the rise and divergence of animals, we cannot conclude from this that some early genetic revolution in *Hox* gene appearance and fixation established a rigid developmental motif that has patterned animal evolution ever since (see more on this in Chapter 8).

Holland (1998) has made this very case for *Hox* genes causing the very explosion of animal life, presumably in the Cambrian. The argument rests on the presumption of crucial increases in organismal complexity, which were facilitated by increased numbers of *Hox* genes by polyploidy or gene duplication. The important transitions (Holland 1998) are:

1. Origin of multicellularity
2. Origin of two-germ layers and radial symmetry
3. Origin of three-germ layers and bilateral symmetry
4. Dorsoventral axis inversion
5. Origin of vertebrates
6. Origin of gnathostomes

Presumably once these innovations occurred, the game was more or less over. Admittedly there are many cases in which the function and sequence homology of developmental genes can be traced over many phyla. But there is equal evidence for a do-all function of developmental genes, complemented and enforced by the action of other batteries of genes that have action more specific to tissues (e.g., neural tube versus surface ectoderm). Temporally, it is clear that developmental genes change roles and specify new positional addresses from one developmental stage to the next. The efficiency of development must increase if a battery of genes is organized by these *Hox* specifier genes, but it is also likely that the downstream gene batteries have an organization of their own, which is also important in development and subject to much variation and evolution.

We have a chicken-and-egg argument to work through. Was the diversity of form afforded by the appearance of *Hox* genes, or were *Hox* genes merely recruited to serve the needs of generating form by switching on batteries of other genes? I favor the following-need model, much like the dauer larva story mentioned above. I admit that we do not have enough information to answer this fascinating question yet. Nevertheless the information we have suggests that the *Hox* gene story is highly complex. The recent discovery that the genes specifying the head region of vertebrates involves recruiting of older genes and the use of newer genes unique to vertebrates only underscores this conclusion (Manzanares, Wada, Itasaki, Trainor, Krumlauf and Holland 2000).

One gets the impression that the *Hox* genes are recruited much the same way a good set of transition chords set up the next part of a jazz song. But once there, as in a good song, the setups (*Hox* genes) are well integrated and the song appears to be seamless. It may therefore be very difficult to solve the chicken-and-egg argument without a detailed phylogenetic analysis of gene expression, right near the roots of the animal divergence tree.

At first glance, the *Pax-6* gene story challenges the recruitment model. After all, if the gene is truly ancestral and has such a conserved function, it strains credulity to believe that it has convergently evolved the same role of eye function again and again. But this result is also compatible with the recruitment model, which would explain conservation of sequence merely by conservation of a general do-all specifier of developmental events, rather than a great innovation in eye evolution. After all, *Pax-6* has complex and variable epistatic interactions with other genes in early development and also is expressed and apparently functions in other parts of mouse and fly development (Halder et al. 1998).

Heanue et al. (1999) demonstrated that the same genetic network employed in eye development is used (with modification and employment of some new genes) to direct vertebrate muscle development. Like the eye network, the muscle network is widespread phylogenetically. This further serves to strengthen the notion of a Hox toolkit, but it is nevertheless clear that the tools apparently work together so well that mutants disrupting specific genetic networks might result in a loss of fitness. To return to the music metaphor, we are keeping the chord progression, because it sounds so good and any alteration will be cacophonous. The answer to the master switch question may be a mixed one.

Developmental Organization and Macromutations

Atavistic features: the whisperings within. Atavisms are coordinated, often incomplete, structures that appear as developmental anomalies and resemble ancestral character states of the taxon to which the individual belongs. We presume that such developmental anomalies often induce already evolved features that are normally suppressed.

The degree of organization and apparent antiquity of atavistic features is often surprising. Consider the atavistic partial limbs of sirenians and cetaceans. The fossil record of the Cetacea is spotty, but early representatives (e.g., *Protocetus,* Middle Eocene) had a well-developed pelvis and sacrum, indicating the likely presence of almost complete hind limbs. Modern whales lack hind limbs. Early Eocene forms have a dentition resembling both carnivorous mesonychid terrestrial mammals (the presumed ancestors of whales) and Middle Eocene forms (Gingerich, Wells, Russell, and Ibrahim Shah 1983). Andrews (1921) described a humpback whale, *Megaptera nodosa,* with hind limbs over 1 meter long. The femur was nearly complete, even though it is normally an internal and diminutive cartilaginous element. Specimens of the sperm whale *Physeter catodon* have been discovered with femur and partial phalanges, even though the femur is normally a rudiment (Lande 1978). If the atavisms of whales and sirenians are any indication, the capacity to reexpress limb elements long lost in evolution suggests that some measure of developmental organization has been retained. Although the final development of a complete limb has been suppressed, the genes or epigenetic subprograms specifying the structures themselves appear to remain to some degree of completeness.

Other atavisms relate birds to their reptilelike ancestors. Kollar and Fisher (1980) placed chick epithelium in contact with mouse (*Mus musculus*) molar mesenchyme. The result was a great surprise. A variety of dental structures appeared, including perfectly formed crowns with differentiated ameloblasts, depositing enamel matrix. For some of the structures to have been produced, the bird epithelium could not have lost, after at least 60 million years, the appropriate mechanism to induce the production of dentin in mouse mesenchyme. This result is grander in scale, but similar to Kurtén's (1963) discovery of the reappearance of an associated group of dental structures, sometimes including the second molar, in the lynx (*Lynx lynx*), otherwise unknown in the Felidae since the Miocene. The absence of complete teeth could be explained either by loss of genes needed to completely specify the structures or by some difference in the inducing mesenchyme. But the genes needed to specify the organized structures have not been completely lost.

Perhaps the most celebrated inference of an atavism was reported in the chick (Hampé 1959). Avian evolution involved a reduction of the fibula, relative to presumed reptilelike ancestors. During the development of the avian leg, the fibula is shortened relative to the tibia, whereas the proximal tarsals fuse with the fibula. These adult features are typical characteristics of the avian limb. Hampé altered the course of development with a series of experiments, such as grafts of fibular primordial tissue, or by insertion of a barrier to equalize blastema size between the tibia and fibula. Two remarkable things resulted from these manipulations. First of all, the chick formed a structure resembling a complete fibula. But when the fibula was completed, it apparently induced contact distally to the joint, reminiscent of *Archaeopteryx*. Muscular development was also altered in an ancestral direction (Müller 1985). In turn, *Archaeopteryx* seems intermediate to the reptilian condition, where a series of ankle bones exist instead of two fused elements at the ends of the tibia and fibula, respectively. Again, the evidence supports the notion that the genes needed to specify structures have not been lost; what has been lost is a switch mechanism that controls their expression.

The common reexpression of such traits suggests the retention of a large degree of organization in either the genome or the epigenetic programs, despite the evolutionary loss of the phenotypic structure. This would be surprising, given that a relaxation of selection should produce a corresponding relaxation and eventual elimination of the genes for the structure (Kollar and Fisher 1980). The retention of genes despite relaxation of selection could be explained by pleiotropic effects on other characters of selective advantage for the organism (Lande 1978). It suggests that some of the organization among genes may be used in yet other structures. The epigenetic reaction to a developmental manipulation, therefore, is somewhat automatic.

As Waddington (1940, 1942) noted, the development of a trait, including the tissue interactions involved, might eventually become so important that the underlying genes might shift with no disruption of the epigenetic outcome. Genes that influence and help to effect the same epigenetic program might come and go. He refers to this process as canalization of development; the developmental program assumes an importance in itself. In cases in which a structure is suppressed in evolution but is reexpressible, it is still possible that the reexpressed epigenetic programs might still be used in the determination of other structures. The preservation of potential for reexpression of the phenotype therefore may not necessarily indicate that the genotype has been exactly preserved. There must therefore be an analogous situation to pleiotropy that has only genetic implications. To distinguish between preserved genes and developmental programs that have widespread influence, we should establish the terms *genetic pleiotropy* and *epigenetic pleiotropy.*

Developmental and evolutionary pathways: jumps across the breach? The preceding sections indicate that the developmental phenotype is a strongly interactive unit, and that evolutionary direction is channeled by the previous evolution and internalization of developmental programs. The question arises: Can major new phenotypes spring into being by simple rearrangements of developmental interactions, and can evolution incorporate such major macromutants? The recruitment of developmental gene networks into different developmental pathways (Heanue et al. 1999) should heighten our interest in this hypothesis.

Atavisms have been a center of attention among evolutionary biologists (e.g., Alberch et al. 1979; Gould 1982b; Lande 1978; Raff and Kaufman 1983; Riedl 1978). This interest reflects the feeling that something important must spring from the fact that major traits, apparently long lost in evolution, can be reexpressed by simple manipulations such as rearranging tissue interactions. As Gould (1982b, p. 343) noted: “But the genome embodies an extensive set of latent capacities, some the echoes of distant ancestors. ... Small changes in rates often activate these potentials, and the result is not only a surprise, but often a major one.” The proximate phenomena of tissue interactions are therefore believed to represent the ultimate limitations and potentials that development imposes on evolutionary directions.

The induction of major atavisms seems consistent with the argument that changes in early development can rearrange morphology and may produce major discontinuous macroevolutionary jumps. If an increase in calcium can induce a chick to make ankle bones, the long-lost structures of reptilelike ancestors, then why can’t minor changes cause major saltational jumps in evolution? This impression is only reinforced by major mutants, such as the magnificent *cyclops* mutant of *Artemia salina* discussed above.

The expectation of major jumps stems from an important assumption, which was best phrased by Maderson et al. (1982, p. 307): “Developmental constraints are the basis of many discontinuities and clumpings in organic morphospace. The sparse and clumped distribution of morphology does not represent a set of optima constructed by natural selection from a set of unbounded possibilities.” If this is true, then the major problem of morphological discontinuity among taxa is solved readily. Maderson et al. went on to say that such a point of view is “not congenial” with the traditional notions of the Modern Synthesis, owing to the implied rapidity of origin of novel structures and the nonadaptive nature of evolutionary change under developmental constraints.

The problem with this argument is the fact that the structures themselves, although determined as units, must be integrated functioning units to permit the organisms to survive in the external environment. The evolution of the unit is a different process from the determination of number, symmetry, or position of the units. The evolution of the unitized switch of the dauer larva of *Caenorhabditis elegans,* as discussed above, may have involved a gradual accumulation of the actions of many genes. A developmental switch gene would arise only after the gradual evolution of the developmental unit is complete and would be maintained only by selection of the downstream genes' contribution to fitness.

The same can be said for any structure. Gradual evolution will form the structure, but only then can other mechanisms switch on or off the developmental program invoking the structure's presence (Mayr 1963, p. 220). The quantum nature of development is thus somewhat deceiving. A long process of gradual evolution may be behind the current presence of a quantally determined developmental program. Once the program is evolved, then its burden, in the sense of Riedl (1978), will determine whether it can be shuffled out of the organism's total development or rearranged to cause the combinatorial evolution of already extant developmental units. The same type of misinterpretation was behind the belief that butterfly mimicry consisted of single-step mutations (Goldschmidt 1945a, 1945b; Punnett 1915). Because the entire mimetic morph seemed to segregate as one unit, Punnett believed incorrectly that one gene, accumulated in one step, determined the mimicry. In fact, gradual evolution had resulted in eventual linkage of many genes whose aggregate effect, in combination with unlinked modifiers, produced the mimetic morph. Current quantum status does not indicate quantum evolutionary steps.

The significance of atavisms is rooted in these same considerations. It is often easy to induce novel structures by simple experiments. But this act only induces what evolution has already created. It does not, and could not, propel the organism forward into a new morphological realm. This is not to say that a possible reshuffling might not lead to occasional novel combinations and a rather distinctive organism – a minor hopeful monster, so to speak. But the exhumed structures have already evolved, and this evolution might have been through the cumulative action of many genetic modifications. The major work, in other words, has already been done. That is why the new structure appears to be so organized.

The importance of atavisms is overstated because of the fallacy of looking at a highly evolved system, backward toward ancestral states that have been suppressed in the evolution of new taxa, and then mistakenly inferring a creative force. The complete suppression of these states might have taken millions of years and many intermediates. But a bird is not just a reptile with suppressed features. The evolution of the derived states characterizing the class Aves involves the origin of many new structures, though certainly preexisting materials and developmental programs must have been modified. If lizard epidermis is placed in contact with chick dermis, it does not produce feathers, only scales! Although it is of great interest that the genes specifying ancestral structures are often not lost, mere suppression does not create organized new structures. Looking backward is not the same as moving forward.

The prospect for the single-step origin of wholly new developmental descendants is also falsely enhanced by examining the results of embryological manipulations. Because the formation of so many structures is initiated by tissue contacts, it is possible to create novel structural rearrangements. But the presence of claws on wings comes only from an isolated manipulation; the wider effects of a mutation with such an effect on the entire phenotype cannot be understood properly with such experiments. Broader investigations must be done to understand whether such changes can be isolated or whether they have other deleterious effects.

As a general rule, major developmental mutants give a picture of hopeless monsters, rather than hopeful change. Epigenetic and genetic pleiotropy both impart great burden to any major developmental perturbation. Thus, it is unlikely that mutants affecting any fundamental prepattern in development are likely to produce a functional organism. Genes that activate switches in prepatterns are not sufficiently isolated in effect on other parts of the phenotype to expect major saltations. The cyclops mutant of *Artemia* is lethal. The homeotic mutants of *Drosophila melanogaster* suffer similar fates. The bithorax complex must function perfectly because it controls, at the least, the fate of segments posterior to the second thoracic (Lewis 1978). The *ultrabithorax* mutant converts the first abdominal and third thoracic segments to second thoracic-type segments. But the gene is always lethal in the homozygote. Disruptions (i.e., mutants) have drastic effects on other parts of the phenotype. The *apterous* mutation, for example, causes reduction of wings and halteres. But it also is the basis for nonvitellogenic oocyte development, failure of development of the larval fat body and precocious death, though these effects are alleviated somewhat at lower temperatures (Wilson 1981a, 1981b). The *engrailed* mutant strongly changes the prepattern for the normal formation of the *Drosophila* sex comb. A secondary sex comb is formed. But the *engrailed* gene also affects the formation of wing veins and development of the scutellum. Pleiotropy reduces the likelihood of major switches that escape tremendous drops in viability due to correlated changes.

The problems with the evolutionary potential of atavisms is illustrated by a relatively minor atavism in the guinea pig (Wright 1934a, 1934b, 1935a, 1935b). A polydactyly mutant, *Pollex,* increases the number of toes in the hind limb of the heterozygote from four to five, the presumed ancestral pentadactyl vertebrate limb condition. The homozygote for this allele dies, usually before birth, and usually has even more toes. Other abnormalities are also apparent in a large number of embryonic organs, and incoherent development is especially prominent in the limb buds, brain, and visceral arches (Scott 1937). The introduction and fixation of such an "atavistic gene" into a population would be highly unlikely. Highly complex syndromes of this sort are common in the mutations of major effect studied in other vertebrates. As in *Drosophila,* they arise from the complex pleiotropic effects of the mutant genes (Hadorn, 1961, pp. 140–148, 182–202).

The organization in development is a two-edged sword. On the one hand, the presence of organization indicates that evolution must move along the valleys of Waddington's epigenetic landscape. But organization also is so intricate that major jumps are precluded because of the high probability of producing a major disruption of proper development. Even Waddington's theory of canalization of development

(1942) requires gradual reorganization of the developmental process. Hadorn's (1961) monograph of lethal developmental mutants put it well (p. 304):

> It must also always be kept in mind that normal development requires the co-ordination in space and time of a large number of individual processes. A mutation which causes the slowing down or the speeding up of a single process may easily induce a standstill of development. In particular, if the development of a primordium depends on the organizing function of another rudiment and the inducing stimulus is delayed, the competence of a reacting system which follows its own rhythm may have disappeared. The process of development must make enormous demands on the harmonious co-operation of the numerous individual processes which are originated in the genetic substances of the chromosomes.

Thus, the accumulated evidence suggests that major developmental mutants are of minor portent in evolution. The side effects are drastic. Moreover, the impression created by atavisms and other homeotic mutants is misleading. The sudden appearance of change indicates only current developmental organization, not a necessary path to macroevolutionary jumps.

It might be argued that hopeful developmental monsters are significant in evolution, but nevertheless too rare to be seen in the laboratory. This may be true and is a frustrating problem because special environmental circumstances could indeed have made such monsters frequent and subject to rapid selection during unusual times in the past. But any geneticist interested in major developmental mutants would be delighted to find viable hopeful monsters in the laboratory, given the various tricks usually necessary to keep developmental mutants in laboratory cultures. But, alas, major developmental mutants are invariably sickly and show pervasive deformities. From both theoretical and empirical points of view, hopeful monsters have led only to hopeless mooting.

Although major jumps are probably excluded from the arguments presented above, evolution by quantum, if rather small, jumps, is far more probable. The phylogenetic and developmental analyses of Alberch (1980, 1981, 1983) working with salamanders, suggested that the previous evolution of developmental programs does result in constraints on the pattern and arrangement of already evolved units. Thus, if reduction of the head or the limb is to occur in evolution, certain directions are developmentally more probable (Alberch and Gale, 1983). But the between-population and among-species changes found (Figure 4.26), for example, in *Bolitoglossa,* are rather easy extrapolations of within-species variants (Alberch, 1980, 1983). The stuff of phenotypic evolution is small developmental units of relatively low burden on fitness. Some of these, such as doublings of structures early in development, might eventually have strong evolutionary significance (Raff and Kaufman 1983).

Interaction of developmental units with natural selection in the external environment. Adaptive evolution may involve a conflict between function in the external environment and the maintenance of an organism with orderly development. To clarify the dynamic interaction between development and the external environment, we at least need information on developmental patterns and identifiable selective pressures.

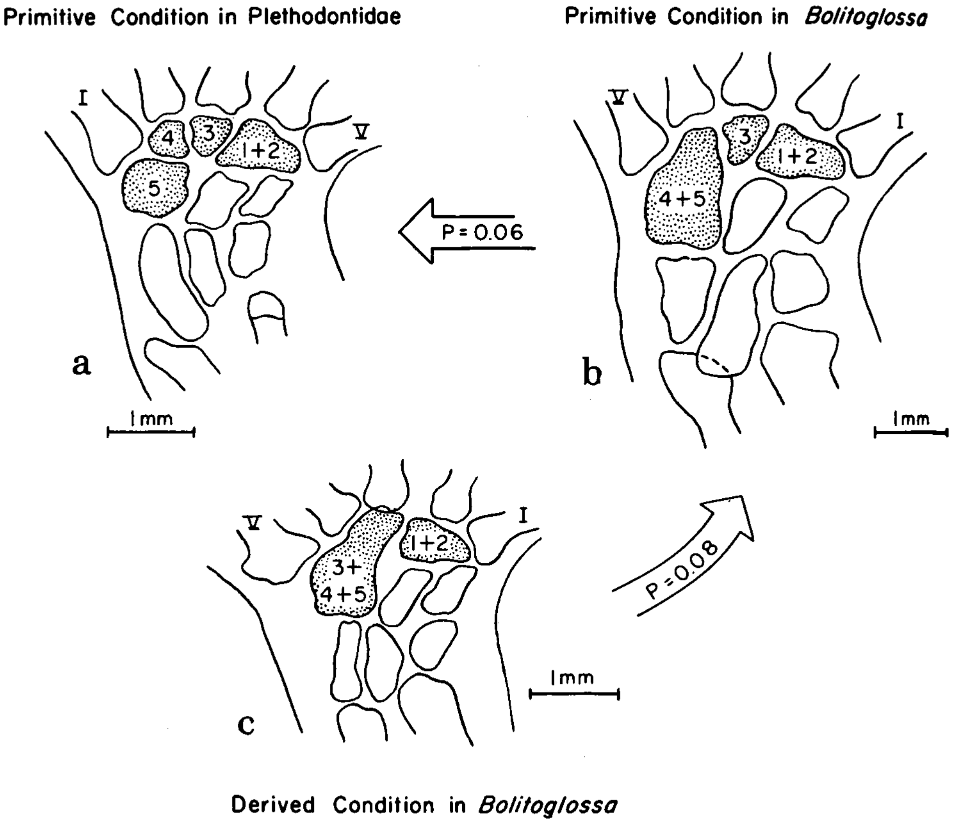


Figure 4.26. Patterns of variation in distal tarsal arrangements (stippled) in *Bolitoglossa,* a tropical genus of salamanders. Intraspecific variation can be extrapolated to interspecific variation. (From Alberch 1980, with permission.)

Articulations in skeletons should be excellent material for such a study. Joints have definable shapes and must function properly for the organism to move properly. Are regularities of distribution the result of developmental constraints or selection? Williams (1950) studied the variation in the cervical articulations among many

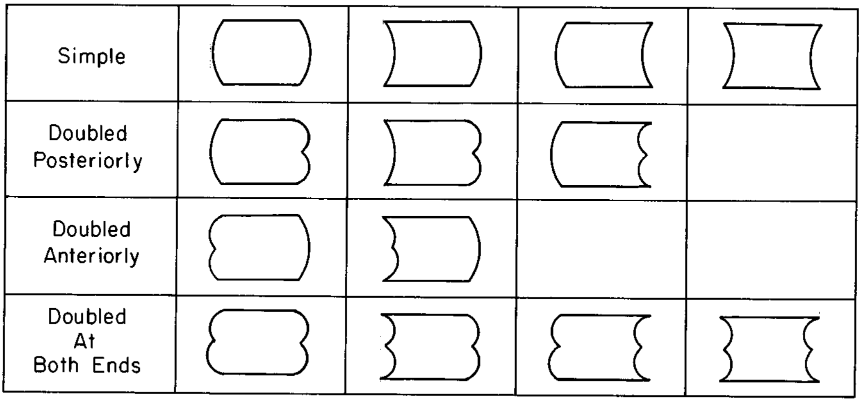


Figure 4.27. Some of the types of centra known to occur in turtles. (After Williams 1950.)

species of turtles and found many regularities that could be ascribed to the interaction of natural selection with the constraints set by the particular joint types. In turtles, the neck is flexible but the rest of the vertebral column is rigid. The neck is therefore the appropriate area for concentrated study.

Figure 4.27 illustrates part of the wide array of possible centra. Some notable regularities arise when comparing species from many families. If a joint involves centra with a single convexity or concavity, there is no variation in the nature of the joint; it is either fully convex or concave. Any structural intermediates would limit the neck's mobility. By contrast, double joints often show intermediates and are often hard to classify. Doubles function by restriction of lateral motion. The same function can be served by changes in angulation of zygopophyses or by mere broadening of the appropriate cervical joints. Changes in doubleness are thus less important in the first place and more easily compensated.

The occurrence of types of joints in the neck is highly nonrandom. Given the 8 joints studied, there should be 2^8 possible combinations of simple convexities and concavities. However, only 16 are observed. Certain centra are never amphicoelous (double concave), joint VI is procoelous in all but two families, and the cervicodorsal joint is either absent or always procoelous. Williams argued that these regularities relate to function. The presence of the procoelous condition, and the absence of opisthocoely, must be correlated with the fact that this joint is the connection between the mobile neck and the immobile cervical column, the most important center of motion in any testudinate. The constancy of joint VI within species and even superfamilies also suggests some functional limitation.

This study raises some important questions. First, the relative action of joint types in articulation seems related to their constancy of form. During ontogeny, cartilage is replaced by bone. Joint cavities are usually determined by in situ lysis of cartilage. First, joint areas are determined, then the nature of the joint. The degree of precision of determination seems related to whether joint function will be impaired. This, in turn, suggests selection as a contributing mechanism to the developmental mechanism of joint determination.

The patterns of cervical articulations present a possibly more complicated picture. On the one hand, certain joints are conserved. A biconvex centrum, always present in the neck, may be a necessity, but its location can be variable. These phenomena would seem to be due to natural selection, because no plausible developmental mechanism would freeze an articulation in one fixed mode. The arrangement of joints, however, is strongly nonrandom and may be interpreted differently. Williams found that certain cervical formulas fixed in one species were to be found as variants in other species. The 16 patterns mentioned above may be related to developmental constraints arising from the presence of developmental fields, inferred by Williams. If we consider the most frequent condition to be the ancestral character state for the group, then deviations can be shown to be of discrete combinations of joint types. Although the general observed increase in procoely from the ancestral condition may be due to natural selection, the path may be controlled by developmental constraints.

The influence of developmental constraint on the course of evolution is evident in the development of the amphibian limb. Alberch and Gale (1983) studied the development of digits in the clawed toad *Xenopus laevis* and in the salamander *Ambystoma mexicanum*. A different developmental order of digit appearance was observed. In the salamander, digit formation was in the order (1-2)→3→4→5. In the toad, however, the order of formation was found to be (3-4)→(2-5)→1. The last digit to differentiate in either case can be suppressed by the application of colchicine, a mitotic inhibitor, during development. This implies a simple developmental mechanism, perhaps reduction of the size of the developmental field. The reduction in frogs, furthermore, seems consistent with the pattern of digit loss found in cases involving the evolution of derived forms with strongly reduced size (Alberch and Gale 1983). This suggests an overall relationship between the pattern of morphological change and the developmental constraint.

Alberch and Gale's results also suggest that developmental rules must be established for each major group, before effective hypotheses can be formulated and tested. In this case, the problem also extends to digit formation, which is enabled by interdigital cell death in reptiles (Fallon and Cameron 1977), but by differential cell growth in amphibians (Cameron and Fallon 1967). This creates strong difficulties in understanding the role of development in extinct groups with no close living relatives.

The study of the ontogeny of the three-spined stickleback *Gasterosteus aculeata* provides an opportunity to combine a developmental and functional analysis (Bell 1981). Lateral plates (Figure 4.28) are modified scales that occur as single bilateral rows. During development, the complete morph passes through stages that resemble, in sequence, the low morph and the partial morph. Bell concluded that the complete morph is the ancestral state and that the other states arose through neoteny. This variation is of strong selective significance, as the anterolateral plates provide the major structural support for dorsal and pelvic spines. In turn, the spines aid in resistance against avian and salmonid predators (Reimchen 1983). Although natural selection is behind reduction of the pelvic vestiges, developmental constraints channel change through a limited set of directional simplifications that often involve paedomorphosis (Bell 1987).

The preceding examples illustrate two main points. First, the knowledge of developmental variation is essential if we are to understand evolutionary directions. Natural selection, however, can be intimately involved in the building and control of the units that are themselves determined by developmental mechanisms. In some cases – the order of development of frog digits, for example – it seems clear that there is no immediate adaptive reason why a particular digit is lost first in evolution. In other cases, however, reduction of given parts will have functional significance relative to the external environment.

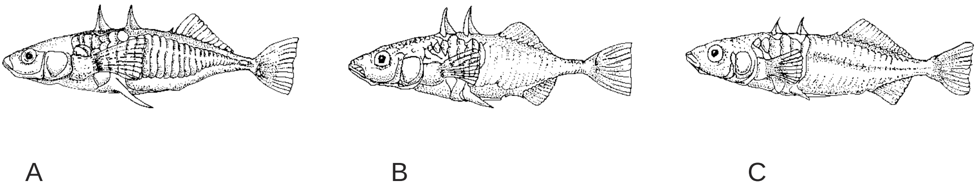


Figure 4.28. (**A**) Complete, (**B**) partial, and (**C**) low morphs of the stickleback *Gasterosteus aculeatus*. (From Bell 1981, with permission.)

The developmental constraints cited above can operate within the context of neo-Darwinian evolutionary mechanisms. If there is a difference, it is the emphasis on the mechanisms designed to form discontinuous structures and developmental mechanisms generating variation. The recognition and understanding of discontinuity is of great importance for the understanding of evolution.

Change of Developmental Programs: Heterochrony and Joint Responses

Order and form in ancestors and descendants. Any violation of the biogenetic law is due to the overall process of *heterochrony,* which de Beer (1958) defined as a difference in order of appearance of structures between ancestor and descendant. This must entail a phylogenetic change in the onset or rate of development of a structure, relative to another. In other words, descendant structures are accelerated or retarded in appearance in development, relative to those of the ancestor. In making such comparisons, some milestone such as the onset of reproduction is employed. It is unlikely that any developmental milestone is very useful as an absolute marker for comparison. The time of reproduction, for example, is itself subject to selection, and varies substantially within and between populations (e.g., Charnov 1982; Stearns 1976). There is no reason to believe that when selection adjusts the age of reproduction, the relative appearance of other structures will be maintained. Indeed, the time of reproduction, overall growth rate, and the relative or absolute time of appearance of structures might all vary in evolution.

To describe changes in order between ancestor and descendant, de Beer devised a cumbersome system that Gould (1977) simplified to the two major processes of *acceleration* and *retardation* of either the time or appearance of a somatic structure or reproductive maturation. The effects of the two processes yielded respectively the patterns of *paedomorphosis* and *recapitulation.* In paedomorphosis, descendants have more juvenile character states at a standard marker of development such as reproductive maturity. In recapitulation, descendants have more “adult” (i.e., terminally added) states at the standard marker. Cases of recapitulation can be consistent with the biogenetic law. Figure 4.29 summarizes some of the various heterochronic states, with a sliding scale showing the descendant’s change in either size, time of reproduction, or appearance of a series of numbered developmental stages. (See Alberch et al. 1979 for a quantitative approach.)

Joint and independent responses. Two different situations of dependence can be imagined. Consider the presence of two independent chains of reactions, whose end products, in combination, produce the visible phenotype. As the two chains can be modified independently, let us term this the *independent response.* Consider a simple model of correlated action, which we shall term a *joint response.* A substance binds to a cell membrane and stimulates the cell to produce a substance that, in turn, switches on a battery of genes. This substance actuates genes in dispersed target cells of varying type (Figure 4.30). We also assume that the genes are switched on after a given amount of this substance reaches the two cell types. A higher rate of production of the substance results, therefore, in the earlier induction of gene action in the two cell types.

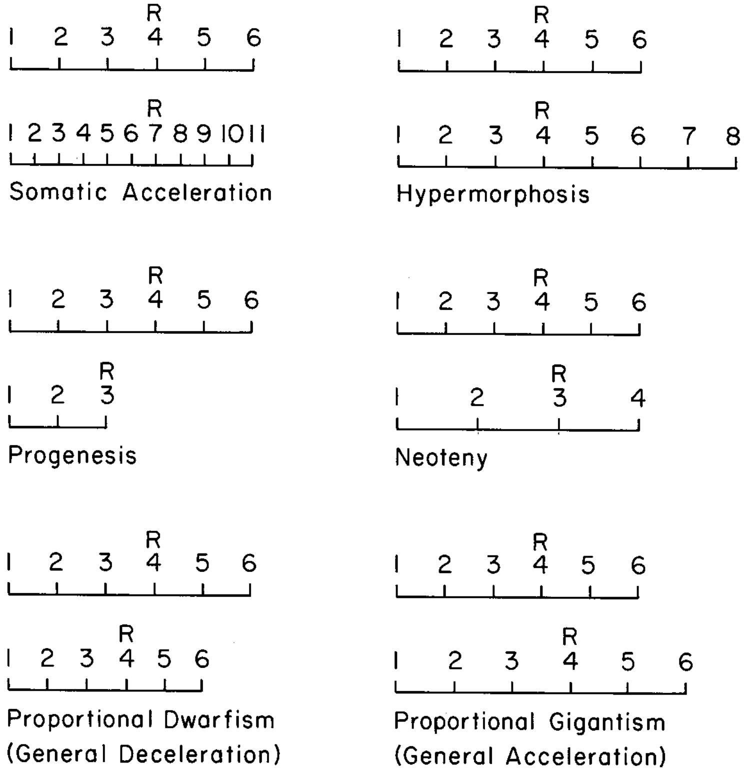
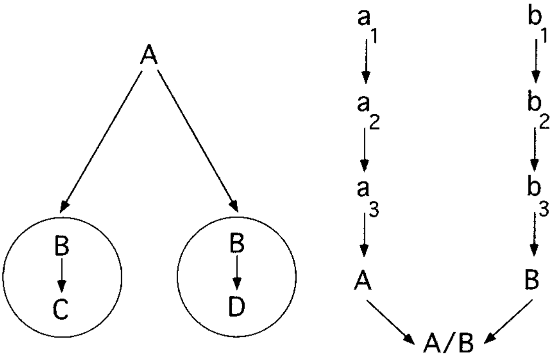


Figure 4.29. Classification of heterochrony, showing outcomes of delay, no change, and acceleration of somatic growth and reproductive maturity. Outcomes of heterochrony are shown on sliding scales.

If a polymorphism for rate of production occurs, genotypes that cause higher production would be expected to switch on the target genes earlier in both cell types. This is the expected correlated response in evolution. This may be an important mechanism for widespread parallel evolution (Alberch 1980).

But what if it is disadvantageous for one of the cell types to be switched on earlier? We might expect selection for a change in the rate of the response of the cell.

Figure 4.30. Two possible developmental interrelationships. Left: joint response, where a single stimulus initiates two separate developmental programs. Right: joint effect of two chains, where the final phenotype is the sum (A/B) of effects of two independent developmental pathways.



The stimulation-inhibition mechanism described above for *Drosophila* suggests possibilities for the evolution of changes in local response. Protein hormones, for example, can be ingested by endocytotic vesicles at the cell surface, and they are eventually destroyed. Different cells will have varying reactions to the same hormone binding to the cell surface. Such differential adjustments might delay or eliminate response by one cell type, to the degree that the gene battery would not be switched on and would become temporally decoupled from other responding groups of cells. In the evolution of life cycles, correlated responses are therefore not guaranteed by developmental constraints.

Metamorphosis in salamanders illustrates a chain of necessary reactions, each of which is subject to modification by natural selection. Three systems are required (Etkin 1970). The hypothalamus produces a hormone that stimulates the pituitary gland. The pituitary produces a hormone, thyroid-stimulating hormone (TSH), which stimulates action of the thyroid gland. The thyroid, in turn, produces thyroxin, which can induce a response in target organs such as the skin. The target organ must be competent to respond to thyroxin. Any disruption or alteration of this chain will delay or eliminate metamorphosis. Evolution, however, could adjust the responses of different organ systems so that the modification of metamorphosis could be organ specific. This is a specific mechanism of evolutionary alteration of a joint response.

The mechanisms of neoteny in amphibians are known to employ different portions of this chain of reactions. In the axolotl, the hypothalamus fails to function (Blount 1950). Injection of thyroxin into the hypothalamus induces metamorphosis. In the genus *Typhlomolge,* a blind, permanently gilled cave salamander, the thyroid is nearly absent, making a shortage of thyroxin the likely mechanism of neoteny. Other salamanders (e.g., the blind salamander *Proteus anguineus*) apparently have normal hormone systems, but the target organs are incapable of response. An addition of thyroxin fails to induce metamorphosis in these forms.

In the axolotl, many characters appear to be juvenile, relative to the presumed metamorphosing ancestor. But the axolotl develops to resemble its metamorphosing ancestor in many other characters such as hemoglobin. Therefore, all characters are not affected as if an entire jointly responding developmental program were arrested by an all-pervasive mechanism. Even though thyroxin can induce metamorphosis, and even though the failure to metamorphose is vested in a single gene with two alleles (Tompkins 1978), the different target organs have evolved an altered response.

At the phenotypic level, the evidence for developmentally correlated change has been best developed by David Wake and his colleagues and students, in their studies of plethodontid salamanders. The neotropical genus *Bolitoglossa* comprises a range of species with strongly varying morphological and ecological features. In highland environments, species tend to be large in body size and have the least amount of interdigital webbing in the genus, whereas lowland species tend to be small and arboreal and have the greatest amount of webbing. Extensive webbing stems from a failure of the digits to grow out of the embryonic pad. Independent digit action is reduced in favor of the total hand or foot action associated with movement of these organisms across wet or smooth surfaces in arboreal subhabitats (Alberch 1981; Wake and Brame 1969). The smaller size and webbing both contribute to adhesion and suction to flat surfaces such as leaves (Alberch 1981).

In some arboreal species, the total phenotype seems to represent a correlated morphological response based on an arrest of overall development (Wake and Brame 1969). Species in the rufescens group have greatly reduced dentition, poorly developed skull bones, reduced phalangial elements, mesopodial fusions, and extensively webbed and flattened hands and feet with sharply pointed digital tips and short tails. In other species, the adaptations of the hands and feet are more independent of the rest of the body. Paedomorphic characters in populations of the Californian black salamander, *Aneides flavipunctatus,* are similar to the latter case, in that a series of pigmentation shifts result from arrested development, but the change goes on independently of others such as those in the vertebral column (Larson 1980; Lynch 1981).

Alberch (1980) summarized the osteological features of the presumed ancestral terrestrial and derived arboreal forms in *Bolitoglossa.* Species bearing the ancestral state have a defined arrangement of tarsal elements (Figure 4.26), with a small minority (6%) of another arrangement. A study of a derived arboreal species shows the predominance of yet another arrangement, with increased fusion. The only variant found in populations of this species is identical to the most common arrangement in the species with the ancestral condition. This suggests that the change can arise from intraspecific variation, and that the polymorphism has small but discrete differences and predictable transformational direction. This is consistent with most known developmentally relevant polymorphisms, which tend to have predictable transformations from one mutant to others (as in the *bithorax* series of *Drosophila*).

Restricted variation is also found in the skull elements of *Bolitoglossa* (Alberch 1983). In some species, the prefrontal bone is lost, as is the third phalanx of the fourth toe. This is most likely due to a truncation of development. In the derived *B. occidentalis,* the only variation observed is in the presence of the prefrontal, making it an atavism. Alberch suggested a general model of phenotype determination quite similar to that of Lande (1978).

Although changes in the rufescens group derive from an overall arrest of development, in other species change is focused on the hands and feet. The latter changes suggest that the entire phenotype is not an overall developmental unit so tightly bound that it cannot be broken up by natural selection. Perhaps strong selection tends to favor larger-scale developmentally correlated changes. If selection is relatively weak, genetic correlations may have time to be broken up.

Some insight on the evolution of a developmental program can be gained by examining the plethodontid salamander genus *Aneides,* which derived from the (American) western branch of *Plethodon* (Larson, Wake, Maxson, and Highton 1981). Here, a gradual evolutionary series can be seen in 10 morphoclines for which the ancestral states can be determined. Nine of these represent dental or jaw characters. Relative to *Aneides,* the maxillary and mandibular teeth in *Plethodon* are greater in number, are short and conical in shape, and fill a greater proportion of the maxillary and mandibular rami. The morphoclines in *Aneides* show a gradual transformation toward enlarged dentition and increased skull strength, associated with the arboreal habit. Unlike *Bolitoglossa,* arboreal forms occupy a perch and so adhesion is not important. In ground-dwelling salamanders of this group, the animal subdues its prey by holding it against the ground. This would be a relatively inefficient method for arboreal forms, as maintenance of perch takes precedence over other activities. This would suggest selection for strengthened jaws and teeth, which would increase the efficiency of seizing and holding prey.

The success of this group involves two innovations: (1) rearrangement of carpals and tarsals, providing for a redistribution of forces to facilitate climbing, and (2) the fusion of premaxillary bones, providing the basis of a strengthened jaw. Both innovations seem to be discrete steps. The overall morphoclines are consistent with the interpretation that the jaw and skull modifications evolved gradually in a series of separate transformations of many small morph features. Larson et al. argued that the intergeneric transformation, although showing a series of intermediates, was rapid relative to the history of either genus.

This transformation series provides evidence that a developmental program can be built gradually, and that the intermediate steps are likely to consist of a harmonious arrangement of the independent characters. Geographic/ecological range extension seems to be important in such evolution. If the most derived forms were subject to evolution by arrest of development, it is possible that the resultant forms would be, in a sense, preadapted for more terrestrial existence.

In conclusion, evidence from the study of salamanders gives a complex picture, ranging from clear nonadaptive joint responses due to evolutionary arrests of development to gradual assembly of functionally harmonious traits into ontogenies molded by natural selection. Even in the case of joint responses, however, intraspecific polymorphism of discontinuous traits of small magnitude is the stuff of evolutionary change.

Ontogeny, phylogeny, and some evolutionary trends. Haeckel's biogenetic law was meant to be a grand scheme, embracing all previous ontogenetic theories, such as von Baer's law (Gould 1977). It asserted that all stages in development were indications of the once-living adult forms of ancestors. Thus, the zygote was to be interpreted as the original single-celled animal ancestor. Swimming larval forms were to be understood as the free-living ancestors of now sessile descendants whose terminally added stages were adaptations for a benthic existence. This scheme ignored completely the adaptive significance of larval dispersal or the functional importance of earlier stages in ontogeny, not as a primordially adult structure but as an important adaptation for juvenile existence.

The universality of the biogenetic law was refuted by the demonstration of rearrangements of the order of appearance of structures between ancestor and descendant (de Beer 1958; Garstang 1922; Gould 1977). This is best encapsulated in de Beer's famous example: Teeth evolved before tongues, yet tongues appear before teeth in mammalian development. The law still strongly influences our thinking, however. A cynical de Beer (1958, p. 7) noted: "It is characteristic of a slogan that it tends to be accepted uncritically and die hard." True though this may be, discussions above tend to suggest that ontogeny and phylogeny might very well be intimately related, perhaps sometimes to the degree that the biogenetic law may hold.

One special set of cases may predict evolution by terminal addition and the subsequent preservation of order. If, as an organism grows larger, a defined sequence of morphological changes best suits it to function within the environment, then those stages might be added in an evolutionary sequence and preserved as adaptive solutions to an ontogenetically ordered series of changing environments. The microenvironment might change for two reasons. First, the organism might be exposed to a qualitatively different microenvironment as it grows larger. A sea fan may live in the turbulent boundary when small and particle feeding would be omnidirectional. As the colony grows up above the bottom, it might be exposed to a unidirectional mainstream current and require a different orientation for its polyps. Alternatively, the organism might actively change habitat during ontogeny. The Caribbean suspension feeding snail, *Vermicularia spirata,* starts out life as a free-living, high-spired, and typically coiled snail. Eventually, though, it attaches to hard substrata, the shell uncoils, and the animal lives as a fixed passive suspension feeder (Gould 1969b). If terminal addition were the mechanism for the assembly of such a series of changes, then phylogeny would assemble the ontogeny by natural selection.

Mollusks and other creatures with accretionary skeletons (e.g., brachiopods, corals, sponges) are natural candidates for such evolutionary trends because the interactions of the shell with the environment are intimate and change continually as the animal increases in size. Phylogenetic trends often indicate a process of terminal addition. This can be seen, for example, in the evolution of the *Athleta petrosa* lineage (Gastropoda, Eocene, Texas). During its history, body size increases steadily (Fisher, Rodda, and Dietrich 1964). The following trends are notable (Figure 4.31):

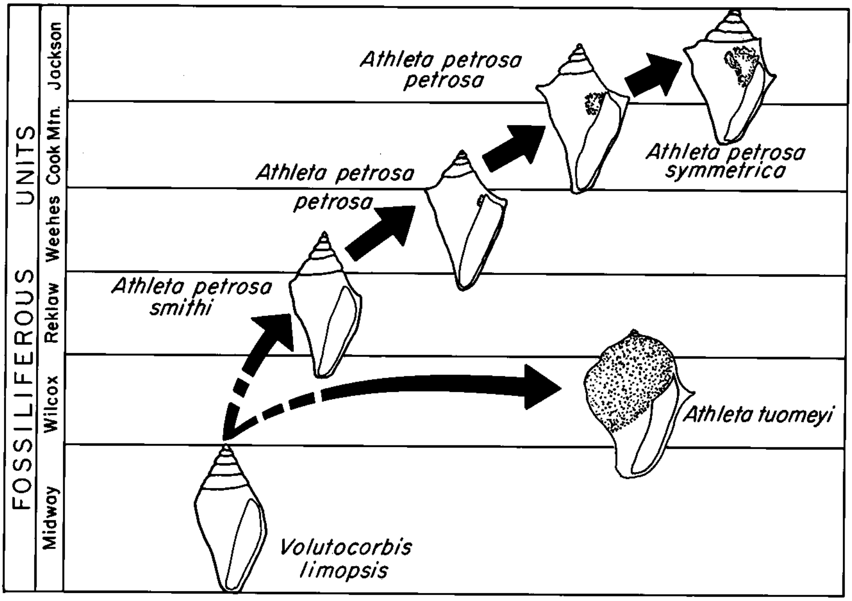


Figure 4.31. Probable instance of terminal addition: expansion of parietal callus deposits in *Athleta petrosa* stock (Eocene, Texas).

- Increase in amount of parietal callus
- Anterior accentuation and posterior loss of spiral lirae on body whorl
- Ornamentation of the sequence *cancellate→nodose→spinose*
- Peripheral elements of ornamentation reduced progressively in number

The appearance of successive stages in ontogeny is accelerated relative to whorl number during the phylogeny. The trends include changes in continuous characters such as linear dimensions, numbers of spines, and qualitative changes in ornamentation patterns. Thus, very different changes can occur in different characters, suggesting very different patterns of developmental, genetic, and adaptive mechanisms within the same evolving lineage.

The Miocene–Pliocene scallop *Chesapecten* has a similar pattern of addition, although intermediate stages in some cases have been dropped (Miyazaki and Mickevich 1982). As scallops increase in size, they often pass from dependency on byssal attachment to hard surfaces (e.g., sea grasses) to dependency on free movement and swimming. This ontogenetic change in habit is reflected in corresponding changes in, among other characters: closure of the byssal notch, equalization of anterior and posterior auricle length, movement of the posterior adductor toward the center of the disc, decrease of rib strength and number, and increase of the umbonal angle. Through the history of the *Chesapecten* lineage, the evolutionary sequence of character state change of adults follows the direction expectable from ontogenetic change. This is especially clear in the byssal notch and in the equidimensionality of the auricles. Some characters, such as position of the adductors, do not change as expected. Some other trends, such as decrease in rib number between successional species, are relatively constant through ontogeny. The pattern of rib loss during the ontogeny of the most derived species does not mimic a progressive reduction of ribs. Rather, rib number is reduced in the smallest individuals where ribbing is detectable. Therefore, a strict mechanism of terminal addition has not been maintained, though the general model of terminal addition is a useful concept in this lineage.

The second major law of ontogeny-phylogeny is that of von Baer, discussed above and in chapter 2. This law asserts that character states early in ontogeny are more general (i.e., ancestral), whereas states later in ontogeny are most likely to be more special (or derived). The embryos of related forms resemble each other only because of the lack of change of earlier embryos in phylogeny, and not because they represent stages achieved by adults of ancestors. Though the law derives from a conception of archetype (represented by the embryonic state), it still makes some sense from developmental and phylogenetic perspectives. This law is likely to have more generality than the biogenetic law, because the stringent requirement for retention of all intermediate stages is relaxed. The biogenetic law, however, can be considered a special case of von Baer's law, as a phylogenetic-ontogenetic order could still be built up through terminal addition (Gould 1977).

The likely modification of later stages in development, relative to earlier stages, is supported by the argument above for a developmental ratchet. Stages incorporated earlier into a developmental sequence may be more difficult to eliminate. Early stages may serve as epigenetic inducers of later stages. Genes affecting early stages of the development of a given structure, such as the vertebrate limb, might have pleiotropic effects on other developmental systems. Structures appearing early in development might be functionally important, to the degree that they literally support later structures (Lande 1978). Thus, the loss of a femur might occur only after more distal and functionally dependent parts were lost in evolution. Finally, simple developmental mechanisms might cause distal, and later formed, parts to be lost before proximal, and earlier formed, parts. The order of digit loss in vertebrates, for example, might depend mainly on the order of appearance in development, which, in turn, may not have an adaptive explanation (Alberch and Gale 1983). Whatever the specific explanation, the evolution of limb loss in vertebrates is consistent with the loss of successively more proximal–early developmental structures (Lande 1978).

Although a fair correspondence can be drawn between developmental phenomena and von Baer's law, the law applies most specifically to the overall pattern of ontogeny, rather than to individual developmental systems, such as the vertebrate limb, or determination of pattern in mammalian coat colors. As we have seen above, there appear to be no real constraints on making major alterations in early development that have necessary consequences for adult form. On a smaller spatial scale, however, it makes sense that order matters in developmental sequences and that later events might depend quite strongly on earlier spatially related events. Therefore, it seems reasonable to formulate a more specific ontogenetic-phylogenetic law, which I term the *law of distal-terminal transformation*. This law makes the following assertions:

1. Many major structures have some form of integration through development.
2. The development of the structure involves an order of appearance of substructures (as in the proximodistal elaboration of the vertebrate limb).
3. When an order exists, evolutionary modifications tend to favor developmentally later stages first.
4. Genetic, functional, and epigenetic considerations suggest that distal parts should also be developmentally last, and therefore most subject to modification. Developmentally later stages, in general, probably are of lower burden and are most subject to change.

Paedomorphosis or recapitulation: which has more potential? G. de Beer (1958) suggested that paedomorphosis had more evolutionary potential than what he called gerontomorphosis, or the extension of a life cycle by addition of developmental stages (hypermorphosis). The addition of developmental stages is associated with ecological specialization and, therefore, evolutionary restriction. Gould (1977) used the Irish elk, *Megaloceras giganteus,* as an example of the largest representative of a clade with less potential than a smaller form with more diminutive antlers. If increasing size can be equated with increasing specialization, then Cope's rule – that size increases during the evolution of a clade – can also be interpreted as a trend toward increasing specialization (Stanley 1973c). Decreases in size would move the clade toward more generalized forms with greater potential for evolutionary change.

On developmental grounds, there *is* reason to believe that the alteration of early development will have more global effects on the organism. This will occur in those cases in which development is sequentially compartmental, as in insects (Garcia-Bellido 1975). However, mutants of early developmental stages may also result in low viability, because such mutants will affect the entire body. On the ecological level, however, there is no reason to believe that mutants affecting early stages of development will necessarily have greater ecological significance in evolutionary change. This depends on the nature of the morphological change.

Accepting a relationship between the addition of stages and restrictive specialization implies that a neotenous descendant is inevitably more unspecialized and therefore of greater evolutionary potential. G. de Beer (1958) argued that the insects might have arisen from an arrest of development of a Myriapod-like ancestor that otherwise would have added segments with limbs during development. Because, as discussed above, the number of segments in long-germ-band insects is determined en masse by a prepattern early in development, the question of paedomorphosis may be irrelevant. Any change in segment number, be it an increase or decrease, involves simultaneous, not sequential, determination at an early stage of development, even if short-germ-band insects have slightly different developmental mechanisms.

Although the hypothesis of enhanced ecological potential of paedomorphic forms is occasionally plausible, it is not clear that it is universal. Common examples tend to be in vertebrate lineages where size increases over long periods of time. Because the earlier representatives of the clade lie phylogenetically closer to the more general ancestors that gave rise to a great variety of vertebrate groups, we tend to think of earlier, more "juvenile," and smaller representatives as being more ancestral and with greater evolutionary potential. This must be true from the taxonomic perspective, because taxonomic rank, a tautologically integral component of one's perception of evolutionary potential, increases inevitably as more plesiomorphic ancestors are considered. Because we know, from our retrospective view, that many descendants arose from given stem groups, it seems reasonable that paedomorphic events should increase evolutionary potential, in the sense of taxonomic potential. But this may not be true of ecological potential, nor may it be true of even overall morphological potential at smaller taxonomic levels.

Does an addition of ontogenetic stages automatically decrease ecological and morphological potential? Consider the *Hinnites* group of pteryoid bivalve mollusks. During ontogeny, animals pass through a shelled stage resembling a scallop, with many ribs and typical auricles. Later, however, the scallop cements to the bottom and continues to grow in an irregular oysterlike form. We can assume that this represents a case of hypermorphosis. As an exercise in fortune-telling, consider the potential of this species if progenesis occurred. A scallop would develop, much like other scallops. It is hard to imagine any unleashing of evolutionary potential. But what if an apparent trend toward hypermorphosis continued. An oysterlike form might give rise to a wide variety of irregular forms adapted to varying hard and soft substrata, embracing the current broad distribution of oysterlike bivalves. Indeed, one possible descendant might evolve a symbiosis with algal symbionts, such as zooxanthellae. This would yield an analogue to the rudistid bivalves, a Cretaceous group that dominated tropical reefs and often reached sizes of 1 meter or more. The hypermorphic or accelerative addition of ontogenetic stages might lead to a large radiation of sessile forms. Because this group has been around since the Jurassic, we can conclude that such potential does not guarantee a radiation like that of the rudistids.

Some of the celebrated neotenous amphibians give no clear indication of enhanced evolutionary potential. They are restricted to habitats of equal or even greater ecological-morphological specialization. The fixed aquatic habitat of neotenous salamanders such as the axolotl gives them no obvious latitude for evolution over terrestrial forms. Neoteny in salamanders such as the genus *Typhlomolge* places them in an evolutionary cul de sac as specialized, depigmented, and blind cave forms. Neoteny can therefore be a dead end in evolution. It should also be remembered that such neotenous forms are "adult" in a wide variety of other characters. True cases of progenesis are probably rare.

A similar argument can be made for the crustacea. The Cephalocarida are the most primitive crustaceans known currently. The degree of specialization of the first three pairs of limbs is far less than in the other extant crustacean groups. Throughout the history of the free living Arthropoda, the degree of limb specialization has increased sigmoidally (Cisne 1975). Taxon survival, however, has not decreased with increasing degree of specialization (Flessa, Powers, and Cisne 1975). This may stem from a similar lack of correspondence between limb specialization and ecological specialization. The cephalocarids are specialized ecologically and are confined to suspension feeding on soft sediments (Sanders 1955). Morphologically specialized decapods, however, range over a variety of habitats from soft muds (e.g., many species of fiddler crabs, callianassid shrimps) to the interstices of coral heads and sponges (e.g., some grapsids, snapping shrimp). Crabs range from deposit feeding (fiddlers and hermits) to carnivory (e.g. portunids), but single species can embrace the gamut. Ecological potential is therefore not necessarily correlated with degree of ontogenetic specialization, because a despecialization does not guarantee more ecological directions.

The cherished belief in the potential of paedomorphs probably stems from the still powerful influence of the biogenetic law and von Baer's law. We still envision development as the unfolding of a phylogenetic series. It is only natural to believe that paedomorphosis peels off the layers of more specialized descendants and therefore begets ancestors with great potential for giving rise to a variety of descendants. Such a prejudice ignores the commonly pervasive evolutionary change of all stages of development.

Although paedomorphosis may not beget increased evolutionary potential, we are left with the apparent fact that many extinctions in the fossil record seem to eliminate relatively specialized forms, and subsequent radiations derive from relatively small-bodied, unspecialized ancestors (Stanley 1973c). A possible explanation is the *extinction of advanced forms hypothesis* (Figure 4.32). Here, we argue that highly derived forms have evolved strongly specialized life cycles and are unlikely to increase potential by heterochrony. Primitive groups, however, may survive and coexist with the derived forms. During an extinction, we would expect that more advanced forms, being more restricted both ecologically and geographically, are liable to disappear preferentially. Primitive forms, having survived the extinction event, will now invade a variety of new habitats and have an opportunity to radiate via a combination of cladogenesis and adaptive evolution.

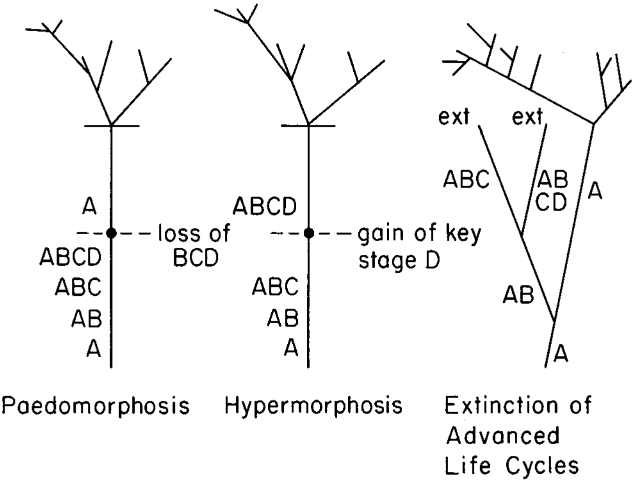


Figure 4.32. Three models of increased evolutionary potential. A, B, C, and D represent character states acquired by terminal addition.

The preferential extinction of advanced forms is a common feature of cycles of extinction and reradiation. A useful example comes from Smith's (1981) summary of the history of Late Cenozoic freshwater fishes of North America. Though the Mississippian fauna was relatively little affected, the Pleistocene caused extensive extinction in the western mountain regions. The most severe extinction is associated with the disappearance of the Glenns Ferry stage of fossil Lake Idaho, where 28 species were reduced to 10 to 14. This extinction focused on more specialized forms such as the large whitefish *Prosopium prolixus,* the most derived form in terms of size and jaw morphology. Forms that survived were more generalized and included primitive salmon, trout, smaller whitefish, suckers, and sculpins.

This model is also supported by the iterative evolution of the planktonic foraminifera in the Cenozoic (Cifelli 1969). Mass extinction passed ancestral globigerinid forms and focused on more specialized morphologies. The progenitors of the succeeding radiation of specialized forms were derived from the surviving primitive generalists, not from specialists who were highly modified by a process such as paedomorphosis. In sum, the real issue of evolutionary potential is the question of selective extinction and potential for radiation of forms who had not changed until an opportunity arose, for leaving a new diversified array of descendants. Evolutionary potential stems from opportunities presented to surviving ancestral forms, and not usually from paedomorphic shifts by advanced forms.

The Main Points

1. Development imposes an internal organization that may be as important in evolution as interactions with the external environment. The internal order may produce developmental constraints, which allow channeling of evolution in a restricted number of directions.

2. Structures arise in development through a complex sequence of changing and localized gene expression and spatial interactions. Developmental mechanisms have evolved to determine complete structures; various threshold mechanisms suppress incompleteness of form. Models of evolution, therefore, must incorporate thresholds and deal with discontinuity in evolutionary change of traits.
3. Evolutionary mechanisms must incorporate the historical constraints of previously evolved spatial interactions and account for completeness of structure. Although development imposes constraints on evolutionary directions, developmental interactions can be broken up by natural selection.
4. Molecular signals such as transcription factors and cell communication factors are widespread throughout the metazoa and have surprisingly similar and usually homologous functions in the initiation of or signalling within developmental pathways.
5. Evidence derived from molecular studies of developmental genes tell a complex story. On the one hand, the *Hom-C/Hox-C* gene complexes depict a unity of gene order and anteroposterior expression that has lasted for hundreds of millions of years. On the other hand, however, many of these genes have generalized functions (setting off batteries of other genes) and might have been recruited independently into many developmental functions. Because the search by developmental biologists tends to focus on similarity of gene function, we may have a view that is biased against variation.
6. It is unlikely that major saltational jumps in evolution are likely to arise even though many structures are seemingly invoked by simple switch mechanisms that often form discrete and monstrous mutants. Such switches have both genetic and epigenetic pleiotropic effects of sufficient magnitude to produce strongly deleterious side effects. This may be why the *Hom/Hox* axial-morphology-determining complex appears to be so stable.
7. Most likely, currently discontinuous developmental events were built up gradually and in continuous interaction with the external environment. On completion of the evolution of the developmental program, it may have been internalized – that is, insulated from direct interaction with the external environment. Developmental “master” genes may integrate or at least set in motion the program that allows the genes that have been built up gradually.
8. In cases in which such a process is involved with ontogenetically changing morphology, a rapid shift toward juvenile forms may simply select for a phenotype that is adapted permanently to an environment suited to the juvenile stage of the ancestor. The biogenetic law – that ontogeny recapitulates phylogeny – probably never holds completely but is most likely to apply when a series of successive phenotypes during ontogeny is each adapted to a different environment. This seems likely in organisms with accretionary external skeletons, such as the mollusks.
9. Paedomorphosis is believed to be a major mechanism for increasing evolutionary potential, but paedomorphs seem no more ecologically versatile than their ancestors. It is more likely that highly derived (= specialized) forms become extinct, and their ancestral, more ecologically unspecialized ancestors survive to give rise to subsequent radiations of specialized descendants. Increased specialization does not necessarily involve increased ecological specialization.

CHAPTER 5

The Constructional and Functional Aspects of Form

> You cannot fly like an eagle with the wings of a wren.
>
> – William Henry Hudson

I loosely follow the prescription of Adolph Seilacher (1970, 1973, 1979), who coined the term *constructional morphology,* to argue that form in organisms evolves under the combined influence of

1. How a structure might be formed by nature of the materials (and, I would add, developmental scheme)
2. Phylogenetic origin, meaning the ancestral character states belonging to immediate ancestors, and
3. Adaptation, as guided by natural selection

This spirit of this very reasonable explanation of phenotypic evolution is also to be found in Jacob's (1983) idea of tinkering, which admits to the eccentric history of evolutionary pathways and co-optation of structures for new functions. The extremists (e.g., Gould 1997), however, would have us believe that nonadaptive aspects of form have been woefully neglected. They claim that evolutionary biologists have sought adaptive explanations in every structure they encounter, to the extent that the structures are perfectly shaped by evolution to perform a function in the very best way possible (Gould and Lewontin 1979; Lewontin 1978). This point of view is a misunderstanding of typical biological practice, fueled by an overly idealized view of biological science. It is true that when seeing a structure for the first time, nearly all biologists ask: "What does this do?" Thus has the function of so many previously mysterious structures (e.g., islets of Langerhans, Golgi bodies) been eventually discovered. Such an approach is surprisingly conserved in all areas of biology, from the subcellular to the whole organism (e.g., what does the springlike backbone of the cheetah do?). That is because it has been so universally successful. Evolutionary explanations certainly follow this phase of discovery.

It is not particularly controversial that the evolution of form is a constructional process, much like the evolution of the modern radio, which still looks much like the original version, but whose chassis is now festooned with transistors, chips, and digital light-emitting diodes, where tubes, analogue tuners, and lightbulbs used to lurk within a very similar cabinet. It has turned out that the *functional program* (what really has been going on as opposed to the straw man *adaptationist programme* of Gould and Lewontin) has worked pretty well. The evolution of function is a very difficult subject and little is added by emphasizing deficiencies without useful alternative programs for research. It is not unusual for antiadaptationists to take such a nihilist approach.

Perhaps the height of such nihilist thinking was expressed by Gould (1983a), who urged us to consider that only a few well-studied examples of natural selection exist. Passing over the truth of that for a moment, he further argued (1983a, p. 90):

> The adaptationist context of current theory leads us to focus upon established examples, but how often do we find any discussion, or even acknowledgment of the hundreds of other unexplained differences that separate most taxa?

Like any politician running for office, Gould wants to convince you that the "undecided" members of the electorate will *all* vote for him.

We need a scheme that avoids rhetoric and allows us to understand the functional context of evolution. How do we judge what is the best function? How do we judge among alternative functions? How do we understand the macroevolutionary consequences of adaptation? How do we distinguish between adaptation and habitat selection of the best fit of an organism to alternative resources? These are the difficult questions that are the main content of this chapter.

We can assign a fairly straightforward flowchart to the study of adaptation and to the functional aspects of form:

1. Identify the structure in the taxon in question.
2. Find out what it "does."
3. Establish a tree of relationships of related taxa.
4. Identify the character states that are ancestral to the taxon in question.
5. Use these character states as part of a set of boundary conditions to determine, if possible, an optimal set of structures to perform the function.
6. Compare the actual structure with the optimal structure.
7. Using the tree, establish a relationship between the appearance of such functioning structures and the presence of the function (e.g., relationship between a robust snail radula and feeding on tough foods); determine whether there were multiple independent appearances of the trait, coincident with the function.
8. Again, using the tree, examine the consequences of the appearance of a trait, with regard to taxon longevity, diversity, or other measures of success.

Performance of Organisms and Adaptation

The engineer's ideal. If the world were simple, if all environmental challenges were unidimensional, and if all organisms had boundless evolutionary potential, an organism's overall form might evolve to be the realization of an engineer's design, fulfilling perfectly a series of functions, such as vision and locomotion. We are attracted to this image of perfection, despite our knowledge of vestigial organs and polymorphism. (The latter can imply more than one solution to the same overall environmental problems.)

Perfection happens. Consider the form of the lens in the eyes of some trilobites (Figure 5.1). Most trilobites have typical arthropod eyes with facets and ommatidia (Clarkson 1979). The eye consists of a series of units, arrayed in a honeycomb pattern of varying shapes and orientations, which defines the visual field of the extinct organism (Clarkson 1966, 1979). One presumes that the overlapping fields of the individual units were integrated to give a mosaic image, but each ommatidium was likely separate in signal from all others; the integration probably occurred in a central ganglion.

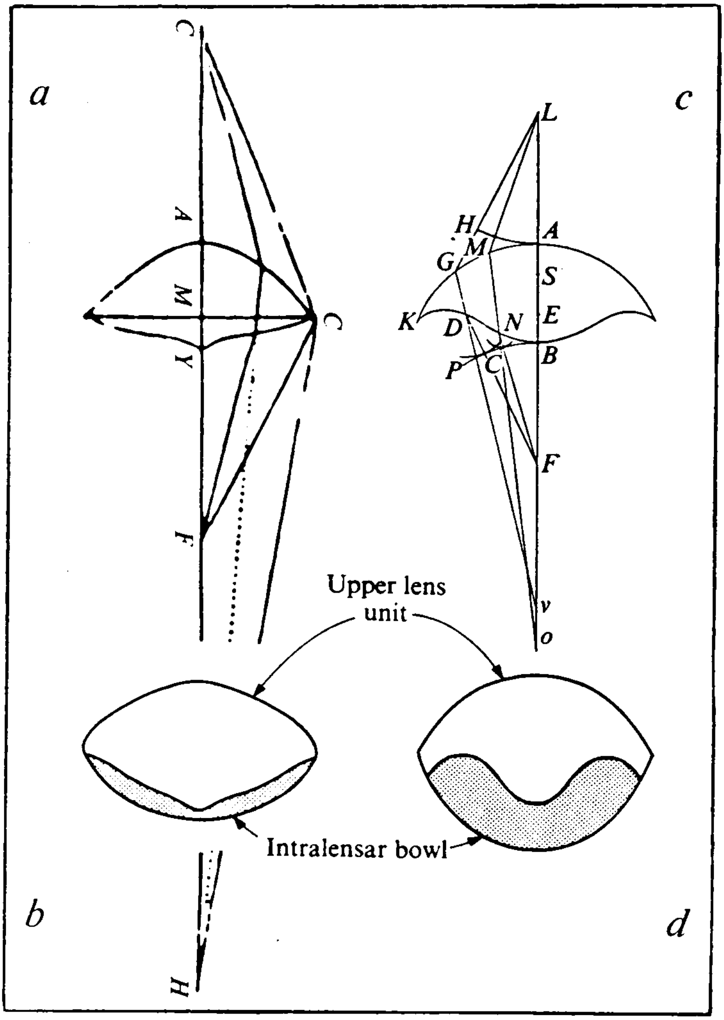


Figure 5.1. **(A & B)** Original construction of aplanatic lenses by Descartes and Huygens, as compared with lenses of the trilobites **(C)** *Dalmanitina socialis,* and **(D)** *Crozonaspis struvei.* (From Clarkson and Levi-Setti 1975, with permission.)

Two trilobite genera have schizochroal eyes, in which a calcite lens is composed of an upper and a lower unit. The symmetry axes of the lens crystals are parallel to the direction of light transmission. Clarkson and Levi-Setti (1975) discovered a remarkable resemblance of the upper lens units to the glass lens designs of Descartes and Huygens, published over 300 years ago, but the trilobites had scooped them by several hundred million years! The human designs sought to reduce spherical aberration. The lower units in each trilobite lens, missing from the human designs, compensated for light transmission through seawater.

If only all structures were so clearly perfectly functional. Mostly, we have the feeling that organisms are performing pretty well, but we are more taken by the eccentricity associated with (1) phylogeny and (2) conflicting functions. When a scallop swims, we know that it has taken its ancestral shell attachment musculature mantle cavity and mantle fusion and adapted this to the production of a jet of water, by means of squeezing the water in the mantle cavity through two small openings. Is this the best way to swim? Ask a fish! Clearly, the swimming mechanism is constrained by the overall bivalve reclining suspension feeding lifestyle, but we can't help but notice that natural selection has fashioned available bivalve materials to perform the function of swimming. In other cases, it is clear that compromises are being struck but more because of mixed objectives of even the same function, such as swimming. For example, a continuously swimming fish is liable to be streamlined and muscular, whereas a fish maneuvering within small spaces will more resemble a disc, with high pectoral fins for turning in tight quarters. But most fish are probably compromises between these two end members of form (Webb 1984). When sudden acceleration is necessary to capture prey, even more complications of form arise.

The probable lack of many instances of pure engineer design to fulfill a simple function complicates our interpretation of structures of extinct organisms. In paleontology, functional morphology is usually as efficacious as the existence of living analogues. For example, Stanley's (1972) excellent study of the functional significance of changes in bivalve faunas through time depends on a knowledge of living bivalves. When fossils bear structures unknown in living organisms, we are suddenly left in the dark.

An ordination principle for inferring function. Suppose that we wanted to know something about the function of a structure of an extinct species. Let's face it. We are not going to often encounter situations like the lenses I discussed above. Also, there are going to be structures that are inpenetrable to our insights: As big and as conspicuous as they may be, we may never know for sure what the sail of *Dimetrodon* really did. But that does not mean that we cannot approach the function of most other structures with a logical and functional approach. This works best when we know overall what the structure might do (e.g., horns of a large vertebrate) but we need really to know exactly what was specifically the function of the structure (e.g., function of the horns of ceratopsian dinosaurs with no sexual dimorphism).

One useful approach is comparative, where both gradients in environmental features defined from the rocks and morphological features defined from a suite of related species preserved in those rocks can be matched with a functional-environmental *ordination function*. Consider the following situation:

1. We can identify an environmental gradient.
2. We can identify a gradient in a morphological feature.
3. We can characterize the performance of a structure in a group of species in terms of the environmental gradient.

If the ordination of performance matches the environmental gradient, then we may conclude that the features of the structure we examined are concordant with differential performance in the different environments, with each trait of a given species matching its respective environment better than other species under consideration.

Consider the following example of vision in trilobites (McCormick and Fortey 1997). The genus *Carolinites* is found widely in all facies of Lower Ordovician sedimentary rocks. Also, specimens are found generally preserved with blind trilobites, which is suggestive of general low light conditions (Figure 5.2). By contrast, the genus *Pricyclopyge* is found in more restricted facies, corresponding to shallower habitats than those of *Carolinites*. These trilobites probably had an apposition compound eye, meaning that each lens is a separately innervated optical unit.

Optimum compound eye design theory uses measured lens diameters and interommatidial angles to determine the so-called eye parameter, which is calibrated against living aquatic arthropods and can be used to gauge the approximate optimum level of illumination for the eyes of these trilobites. The appropriate calculations suggest that *Pricyclopyge*'s eye dimensions correspond to stronger light conditions than those of *Carolinites,* which fits their relative habitat occurrences. We thus are able to adapt optical principles to form a hypothesis ordinating eye morphology onto an environmental gradient.

Generalizing the ordination principle to inferring adaptation. Because we can associate different structures with differential performance in different environments or

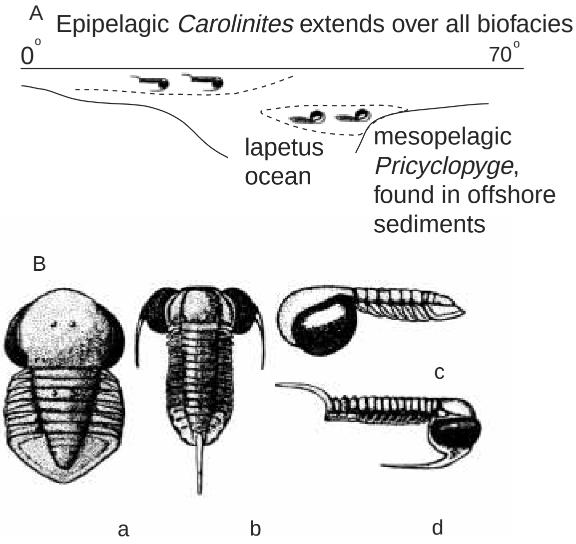


Figure 5.2. Forms of two trilobites. (**A**) *Carolinites* is found in a wide variety of Lower Ordovician facies and probably lived in low-light conditions, whereas the genus *Pricyclopyge* is found in more restricted facies, corresponding to shallower habitats. (**B**) Form of the body and eyes of *Pricyclopyge binodosa* (*a* and *c*) and *Carolinites killaryensis* (*b* and *d*). (After McCormick and Fortey 1997.)

when performing different functions (e.g., swimming versus crawling), we now can ask whether structure–function relationships may be used to infer adaptation. To be specific, let us define adaptation with respect to the acquisition of specific character states X_i that can be associated with function Z_i. If we have a tree (Figure 5.3) where the character states X_i arose several times, we would predict that function Y_i arose in conjunction with those character states.

Such a tree could be constructed from a set of taxa that bear states of character X and are known to perform function Y. For example, we could imagine a group of fish taxa where disclike shape is associated with a known zigzag swimming behavior. This isn't obviously an example appropriate for extinct organisms, but we could, for example, imagine a case in which a clearly deep-burrowing bivalve morphology (large size, elongated, deeply incised siphonal pallial scar) is associated with sedimentary structures connoting the intertidal zone (e.g., ripples combined with mud cracks). We then might ask if there is a correlation between the character states and the environmental occurrence, relative to the same parameters in sister species. Thus, this approach could be applied to extinct as well as living species.

Say there are n taxa and that all taxa with character states X_i also perform function Y_i. We might then associate the character state with the facies in which a fossil is found, which reflects the environment. There is a problem in establishing the strength of the correlation between character–function and environment, because the possible associations of all n taxa with their respective character states cannot be said to have necessarily arisen n times. Indeed, in the worst case, the trait may have evolved only once (Figure 5.3) and the subsequent taxonomic splits faithfully replicated the character–behavior combination. Thus, we would be inflating the number of degrees of freedom in a correlation analysis between character and environment if we ignored the tree structure, which could tell us conservatively how many times the association arose.

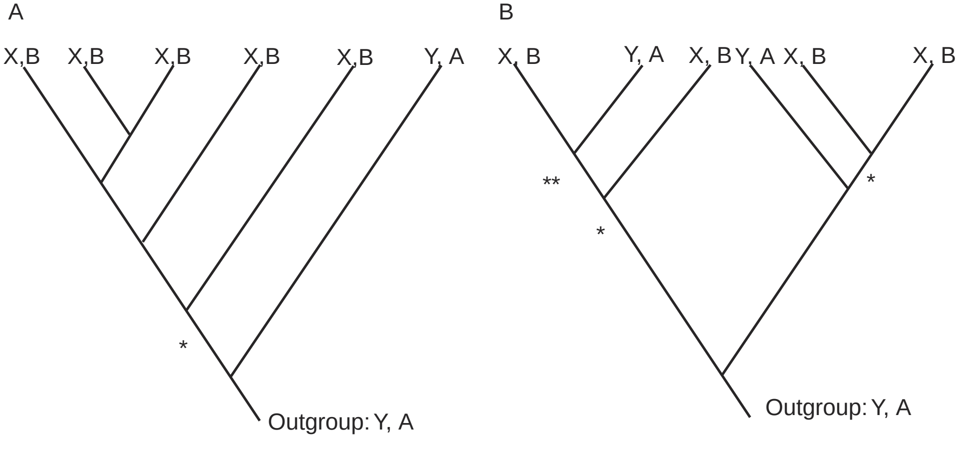


Figure 5.3. Plotting associations between form and environment on a tree to infer adaptation. We assume that character *X* performs best in environment *B* and that character *Y* performs best in environment *A* (*Y,A* is ancestral): **(A)** On this tree, the association *X,B* occurs in five taxa, but it arose only once (*). **(B)** Here, the association *X,B* arose at least twice (*) with one reversal to *Y,A* (**). Therefore, there are three events that are independent and adaptive.

If we wish to test statistically for an association (correlation) between the occurrence of X_i and the environment, it is therefore necessary to take the structure of the tree into account. Following the pioneering work of Felsenstein (1985), a number of methods have been devised to correct for the bias of terminal taxa and tree structure (see Harvey and Pagel 1991), which are summarized in Table 5.1. These are collectively known as tests using the *comparative method,* a general approach originally used by traditional systematists to qualitatively examine the evolution of adaptation in different parts of an evolutionary tree.

As an illustration of the establishment of adaptation from the association of character states with a behavioral trait, consider the feeding biology of wrasses belonging to the group Cheilinini (Westneat 1995). The lever and linkage mechanics of the jaws of these fishes are strongly correlated with feeding, which may take the form of pursuit feeding on evasive prey such as other teleosts or feeding on relatively immobile hard-shelled prey such as gastropods and bivalves. As might be expected, displacement advantage is greater in wrasses that seize evasive prey.[1] A principal components analysis demonstrated that the jaws of species that feed on hard prey are largely distinct from those that feed on evasive prey.

The evolutionary tree demonstrates that the acquisition of the habit of feeding on evasive prey arose four times in the history of extant forms (Figure 5.4). Two differ-

Table 5.1. Some Tree-Based Methods Used to Calculate Correlations between Characters[a]

Method	Character Type	Statistical Test
Contingency table	Discrete	Chi-square test of frequency of all branches on which either character changes
Independent states test	Discrete	Chi-square test of frequency of all branches on which dependent character is ancestral or changes to derived
Concentrated changes test	Discrete	Probability ratio of achieving an observed character distribution by random sample
Independent contrasts	Continuous	*n*-1 sister group comparisons, correlation along branches, probability value from simulated null distribution
Squared-change parsimony	Continuous	Least-squares node reconstruction, correlation along branches, probability value from simulated null distributions
Phylogenetic autocorrelation	Continuous	Phylogenetic W matrix multiplied by character vector separates variance due to phylogeny, relative to adaptation

[a] For example, form and environment.

After Westneat 1995 and references cited therein.

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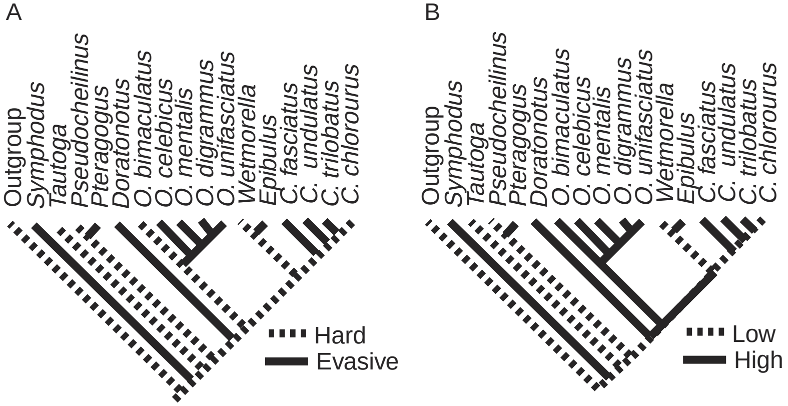
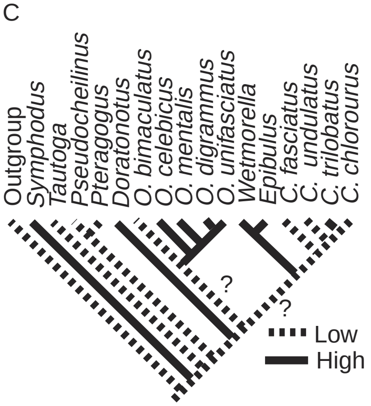
[1] Displacement advantage is the inverse of mechanical advantage and therefore correlated with speed of jaw closure. One would expect to want jaw closing speed to deal with evasive prey but high mechanical advantage in dealing with crushing bivalves and gastropods.



Diet

Displacement advantage
of jaw opening



Kinematic Transmission
of Maxillary rotation and
gape angle

Figure 5.4. A mapping of the dietary habits and two biomechanical characters on a tree of relationships for fishes of the wrasse group Cheilinini. (**A**) Dietary characters: hard or evasive prey; (**B**) hyoid kinematic transmission (KT), biomechanical character; (**C**) maxillary KT, biomechanical character. (Modified from Westneat 1995, with permission.)

ent mechanical jaw indices show a close association between the acquisition of the habit of feeding on evasive prey and the acquisition of the jaw mechanical apparatus required to maximally accomplish this form of feeding (Figure 5.4). Westneat used three different measures of statistical association between the feeding character state and the biomechanical character states and found a significant correlation, which suggests that the four independent acquisitions of the new jaws was adaptive with regard to the change in feeding behavior.

This approach gives us a direct means of assessing the occurrence of adaptation, especially if we have multiple origins of a structure and can reliably score the associated behavior. It does not, unfortunately, do us much good for grander traits that often occur in complexes, such as the mammalian skull, relative to its reptilean ancestor. Thus, as traits become more and more complex, are they less susceptible to this sort of analysis?

While complexes of characters may be more difficult to understand owing to the increased numbers of degrees of freedom of developmental determination and functional directions, they sometimes constrain hypotheses of the evolution of function and evolutionary origin of taxa. Bivalve mollusks use siphons, gills, palps, mouth, and gut to process particles and the functional interactions among these structures constrain their evolution (Levinton et al. 1996). For example, gills of suspension feeders collect particles and must have a large surface area. In suspension feeding bivalves the gills pass on particles to the palps, which may sort and reject poor particles, passing the accepted residual to the mouth. In derived deposit feeders, such as members of the genus *Macoma,* the gill collects particles, but is strongly reduced in size, owing to the reduced area required to collect concentrated squirts of sediment. In these forms the palps are greatly expanded in size, facilitating the increased sorting of a much greater proportion of unacceptable sedimentary particles, which must be rejected. This coupling suggests a predicted association between characters on a cladogram. In microchiropteran bats, there is a coupling between structures associated with echolocation, respiration, and flight (Rayner 1991, Galis 1996). Flight combined with expiration facilitates the production of echolocation pulses. This association supports the integrated set of characters that perhaps suggests a separate evolutionary history of microchiropterans from macrochiropterans.

Optimality: The Direction Adaptation Takes?

Optimality in evolutionary arguments. We must have criteria of performance to evaluate adaptation. The example of jaw evolution in wrasses mentioned above suggests that it is possible to evaluate relative performance of different morphologies when performing a specific function. We usually employ *evolution in the direction of better performance* as a justification for adaptation, but this directionality implies that there is some form that performs the function optimally. When functions and structures are relatively simple, then this task may be tractable, although one must admit that the complex nature of behavior and morphological–physiological function suggests that many cases will consist of complex compromises that are difficult to define analytically.

The perfection or at least interpretability of trilobite lenses leads the brave-hearted to believe that organismal form might be predicted from first principles of engineering design. Rudwick (1961, 1964) developed a formal approach to the study of fossil form based on engineering principles that was meant to solve the problem of inferring the function of structures of extinct organisms with no close living analogues. He believed that for every function, there was a *paradigm structure* that could be predicted from various first principles (Rudwick 1964). “This is the structure that can fulfill the function with maximal efficiency under the limitations imposed by the nature of the materials” (Rudwick 1961, p. 150). If the paradigm fits the structure in the fossil organism, then we conclude that the structure’s function has been found. If

Rudwick's approach is correct, we can (1) deduce function in fossil structures and (2) provide a convincing demonstration that the structure performs the function in an optimal way. Such a fit was evidence to Rudwick of adaptation, or of a historical process that led to perfection of form according to function.

One of Rudwick's primary examples was a detailed study of the form of the richthofenids (Figure 5.5), a group of bizarre Permian brachiopods that typically have a deep conical ventral valve and a much smaller and flat dorsal valve that apparently could seal off the opening of the other conical valve. In a brilliant demonstration of functional inference, Rudwick (1961) proposed that the functions of filter feeding and large-particle exclusion necessitated rapid movements of the dorsal valve to create powerful currents from which food particles could be collected by mantle surfaces. Spines would be required to exclude large particles. Rudwick built a scale model that demonstrated the plausibility of his functional argument.

Rudwick's interpretation has not withstood further analysis. The shell-flapping mechanism required a musculature unknown in brachiopods (Grant 1972). The unusual morphology of an open calcified shell has been interpreted more successfully as reflecting a symbiosis with algae, perhaps zooxanthellae (Cowen 1983).

Rudwick's proposal is a pure form of the argument of optimality in adaptation. If it is taken to the limit, a whole organism could conceivably be constructed from the same principles. Thus, a mammal would be a perfect machine, deducible from a sum of individual functions. I should like to focus on three important assumptions of the argument and show their limitations. These assumptions are: (1) a perfect fit to the environment demonstrates adaptation; (2) the evolutionary change of form is unrestricted by various constraints (Rudwick did not hold this extreme a view); and (3) unique optimal solutions can always be deduced. Although the limitations reject the

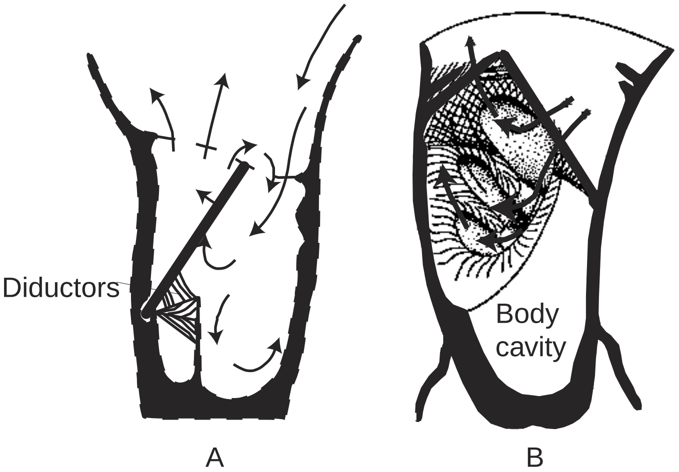


Figure 5.5. Functional interpretations of richtofenid brachiopod form. (**A**) Rudwick's (1961, 1970) interpretation of flapping of the dorsal valve, operated by strong diductor muscle; (**B**) Grant's (1972) opposing interpretation, allowing for a weak diductor and relatively little dorsal valve motion.

pure argument, they often lead to an *evolutionary optimality argument,* applicable only to a narrower range of specific structures and functions that often serves well in evolutionary biology and has been unduly maligned in recent years. Rudwick's (1970) descriptions of the geometric problems of logarithmic spiral growth in the articulation of brachiopod valves show his use of such evolutionary optimality approaches.

The fit to the environment. The match of form to function is used by Rudwick as prima facie evidence for adaptation. This implies that a current static situation reveals a historical process. Is this valid? It might be if (1) the paradigm approach were appropriate and (2) evolution via natural selection were such that perfection is always achieved. The universality aspect of the argument is troubling. After all, Darwin (1859, p. 199) wrote that "natural selection will not produce absolute perfection. . . . [Natural selection] must act chiefly through the competition of the inhabitants with one another, and consequently will produce perfection ... only according to the standard of that country." But what are the standards of the "country" in which a given structure arose? If we see a current match of form to function, can we be sure that it reflects past adaptation?

Consider the data in Figure 5.6, showing a positive correlation between tongue (labellum) length of species of syrphid flies and the corolla depth of flowers. Tongue length is associated with matters of importance to the fly. The proportion of pollen in the diet increases with increasing tongue length. Moreover, longer-tongued flies tend to visit flowers with longer corollae, because the latter tend to contain more nectar than do flowers with shorter corollae. The match of many species in the figure can therefore be interpreted as an evolutionary fitting of tongues to solve the food-gathering function. Why don't all species of flies have long enough tongues to invade the largest and most nutritionally useful flowers? We might invoke the pressure of interspecific competition to exploit the broader spectrum of resources. But something is wrong with any such argument. The flies surveyed have come from an urban garden filled with species usually not visited by the flies. The match is not entirely fortuitous, but it certainly does not involve any long-term adaptation of

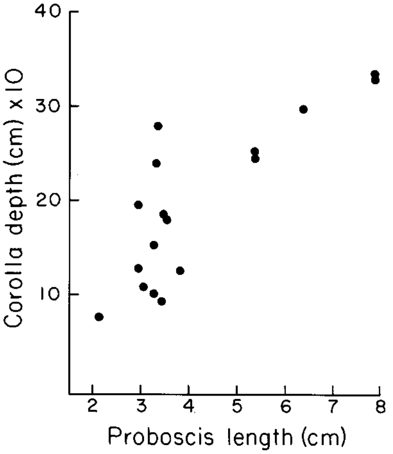


Figure 5.6. Relationship between proboscis length of a number of syrphid fly species and flower corolla depth. (After Gilbert 1981.)

tongue to corolla. Having been thrust into a new situation, the organism has chosen its best environment. With no evolution at all, a fit of (at least one structure of an) organism to environment is achieved admirably.

This example is meant to separate the argument of optimality from adaptation. As a static concept, optimality is a testable hypothesis. One specifies a series of boundary conditions and a series of equations governing the optimal performance of a function. The boundary conditions may often be difficult to establish, but one might safely conclude that structure x_2 is optimally suited to perform behavior y. But this does not prove adaptation, in the sense of a historical process that perfected the structure from a less perfect state x_1. One must have historical evidence of the process of change. This is what we usually lack.

It might be argued that the overall perfection of an organism is proof positive that the fit of an organism to an environment is no accident. If a running, eating, reproducing species lives indefinitely in harmony with its environment, can we not conclude that the totality of the organism's form could not have been produced by a chance choice of this organism in its environment? After all, a horse does well in a farmer's field because it evolved in a similar habitat, not because the farmer chose the one organism in the world that happened to survive in his field.

As more structures are considered, any optimality argument will tend to break down. Conflicting constraints, uncertainty about interaction effects among various structures, and genetic and developmental correlations, will all become more and more intractable. As fewer and fewer structures are considered, the possibility of a functional approach becomes more and more real, but the dangers of the matching argument increase as well. I can't convince you that humans, overall, have adapted to live underwater, but a few aspects of humankind's phenotype – hairlessness and the pelvic skeleton – have been used in a serious attempt, at least to the author, to take an environmental fit argument (e.g., hairlessness implies swimming) and to draw evolutionary conclusions (Morgan 1982).

It is unlikely that the simple alternative of choosing one's optimal environment, based on randomly acquired structures, is a viable explanation for the fit of form to environment. But an interaction process between the organism and the environment must substitute for the usual dualism of an environment and a variable species, with natural selection culling out the poorly adapted forms. Lewontin (1983b) described evolution as an interactive historical process based on a combination of environmental culling and the organism's set of abilities to select its own environment. He has stated four principles:

1. Organisms determine what is relevant.
2. Organisms alter the external world as it becomes part of their environment.
3. Organisms transduce the physical signals of the external world.
4. Organisms create a statistical pattern of the environment that is different from the pattern of the external world.

The points above may bring organisms into complex relationships with their environment, some of which may violate the association that we expect between function and form. I once found a perfectly normal-size and healthy live specimen of the marsh mussel *Geukenzia demissa* living happily on the rocks of West Haven, Connecticut, despite Stanley's (1972) convincing argument that they were adapted to living in the sediment. How that bivalve arrived to survive at those rocks I do not know, but I can assure you that it is a rare event. The rarity is probably related to larval adaptations, rather than a complete inability of marsh mussels to live on rocks or better in cracks between boulders. If a larval swarm were trapped in a rocky lagoon and if larvae could settle on rocks, I would not be surprised to see a large population appear, perhaps only to be outcompeted by some other species. This only reemphasizes Lewontin's point that a complex adaptive framework determines organismal occurrence.

The story of horse evolution is a classic in adaptation and macroevolution, which we owe to the great work of George Gaylord Simpson and his successors. But it also is a story of matching morphology to environment is a fairly simple way. Simpson recognized that horse evolution could be described only as a complex radiation, but many lines shared a trend toward *hypsodonty,* which is a response to the wear on teeth during feeding, particularly grazing on tough grasses. For horses, hypsodonty involves ever-growing and high-crowned teeth (MacFadden 1992, p. 233). From the Eocene to the Early Miocene, horses had short-crowned teeth, which corresponded to a browsing habit, but the expansion of grasslands in the Miocene resulted in a rapid radiation of horse lines, each of which developed more and more hypsodont teeth. A change from clayey soil to sand from the Oligocene to the Miocene may also have been a selective force for hypsodonty (MacFadden 1992, p. 235).

Mammalian herbivores can be broadly classified as browsers or grazers. Tooth wear comprising more scratches and fewer pits is associated with grazing, and the complementary pattern identifies browsing. Also, differences in δ^{13}C between browse plants, dominated by C_3 (Calvin) photosynthesis, and grazed grasses, dominated by C_4 (Hatch–Slack) photosynthesis, are reflected in isotopic deviations found in mammalian teeth. Using living mammals as a guide, Miocene–Pliocene Bone Valley horse species spanned both feeding types, and some of the most hypsodont horses appear to have mainly browsed (MacFadden, Solounias, and Cerling 1999). It is perplexing that one of the least hypsodont species, *Nannippus minor,* was principally a grazer, at least by virtue of wear and stable isotope evidence. The only survivor of the group of coexisting horse species was strongly hypsodont.

This example challenges us in many ways. First, a broader perspective suggests that hypsodonty is not so faithfully associated with the grazing–browsing alternative. Llamas and gazelles are not primarily grazers, yet they are hypsodont. Baboons and kangaroos, although primarily grazers, are not especially hypsodont. We can escape this trap by rejecting Simpson's simple association between hypsodonty and grazing, but we cannot ignore the trend toward hypsodonty observed in the Miocene as grasslands expanded. A disturbing conclusion emerges: Morphological trends may be readily explainable by adaptation, but no particular set of species may be uniquely explainable in terms of absolute values of a particular morphological trait relative to the microenvironment in which the species finds itself. Another way to say this is that we can see a selective force at work when change is occurring, but a snapshot of coexisting species may be harder to interpret.

Exaptation, adaptation, and preadaptation. If optimality is not an argument for adaptation, as commonly supposed, how does one study the process of adaptation in the first place? We must clarify some terminology before discussing this difficult question. *Adaptation* refers to a historical process in which improvement of function by a phenotype is gauged by means of a model assessing the organism's performance. We do not deny the absence of random change, and constraints on the evolution of form. Adaptation only implies a continuity of a function–structure relationship. We invoke no implication of functional perfection but must assume a trend *toward* that perfection to infer adaptation. It is also conceivable that as such a trend occurs, a set of complex interactions among different structures within the organism continually changes the functionally optimal form. There may be no goal, only a treadmill.

The definition of the historical borderline in time between two distinct periods of structure–function relationships has long been the subject of terminological debate and confusion. Consider the following (Bock 1959): The skimmer, *Rynchops niger,* flies just above the water and has a mechanically remarkable beak and musculature that enables it to rotate the lower bill just as it hits the water, enabling it to snatch a fish near the surface without snapping off its mandible. Skimmers have a basitemporal articulation in the skull that is a true diarthrosis. The medial brace formed by the articulation absorbs shock as the mandible hits the water. We can imagine the following historical sequence to result in the evolution of the structure:

1. A change in feeding habit brought on by an abundance of fish living just below the air–water interface who cannot detect predators skimming along the surface above.
2. Selection for increased musculature to deal with the stress on the lower jaw during prey capture.
3. A correlated response involving an increase of the medial process of the mandible for muscular insertion. The medial process thus "approaches" the base of the skull.
4. The proximity of the mandible permits a diarthrosis to develop, perhaps in different places in different bird lineages.

Bock argued that the initial morphological character states borne by the skimmers' ancestors constituted a *preadaptation,* which was that state in which a structure's present form enabled it to discharge its original function but also enabled it to assume the new function, whenever the "need" arose. The preadaptive structures are necessary for the evolution of the structure that serves the new function. But built into this concept is a concept of probability as well. If the new behavior (in this case, skimming) is adopted, bird lineages with the preadaptive structures are likely to evolve successfully to feed in this way specifically and optimally.

The term *preadaptation* is therefore a retrodictive statement. It is a loaded adaptive gun, ready to fire when the necessary situation appears. The exact evolutionary trajectory is unknown, but a general direction can be predicted once the new selective need arises. Some functional continuity is likely to exist between the preadapted and adapted structure (i.e., use of a beak to seize food items).

Gould and Vrba (1982) proposed the term *exaptation* to characterize the evolutionary process where structures are co-opted and modified for a completely new function. This term is meant clearly to provide an alternative to Darwin's solution to the problem of jumps in evolution, posed by Mivart (1871, pp. 142–143), which was that intermediate and apparently nonadaptive morphological stages served other functions than those of the final stage (e.g., in the evolution of winged from wingless forms). The term *exaptation* is thus a specific case of Darwin's solution, to which he gave no name.

In a sense, all adaptation must follow an episode of exaptation. After all, no structure arises de novo, designed to serve a given function. The process of adaptation follows exaptation and involves the evolutionary change of the new structure–function relationship. A molecular example of exaptation is the evolutionary relationship of lysozyme and lactalbumin (see Jacob 1983). Lysozyme is used by vertebrates to hydrolyze the mucopolysaccharides of bacterial cell walls. Lactalbumin has nearly an identical amino acid sequence but is a principal constituent of mammalian milk. In humans, it constitutes the beta chain of the mammary gland enzyme lactose synthetase. The abrupt change of function represents an exaptation.

Although exaptation is a useful formalism, it is quite difficult to apply unambiguously when the function and structure both have changed radically, but perhaps not enough to be considered completely new functionally. For example, the evolution of the Cetacea involves the strong modification of the limbs into flippers. If the functional change from walking to swimming is regarded as completely new, then the rearrangement of skeletal elements in the limb is an exaptation. But if locomotion is considered to be the function, then one might regard the change as simply part of the larger process of preadaptation. Indeed, the predictive concept of preadaptation is quite useful because it delineates the potential pattern of adaptation, should the function change slightly. *Preadaptation* refers not to an exact evolutionary path but rather to a range of possible paths, given the selection pressures (Bock 1959).

Theoretical morphology. Morphological variation can be often be simulated with a fairly simple set of geometric rules. Theoretical morphology is the field devoted to specifying such rules and predicting the range of possible morphologies. To be useful and conformable to biological limitations, the generating equations must correspond to some form of biological growth process, or the geometric rules must not be so omnipotent that they can create forms patently beyond the means of the organism. The algorithms are also accretionary; that is, they describe what the organism must do next to add a new growth increment.

The most important theoretical advance in this field was Raup and Michelson's (1965, Raup 1966) analysis of the coiled shell, based on the knowledge that many organisms grow according to a logarithmic spiral, which generates no change in form as size increases. Thus, the rules of growth are independent of the location of the current accretionary growth increment. This simple situation does not always apply – spatial information must often be provided (McGhee 1980). Still, growth of some planispiral mollusks can be simulated with a computer when the following parameters are known (Figure 5.7):

1. *Shape of generating curve:* Cross-section of the spiraling form
2. *Whorl expansion rate:* The factor by which the size of the generating curve (ratio of successive diameters, if a circle) increases after one complete rotation

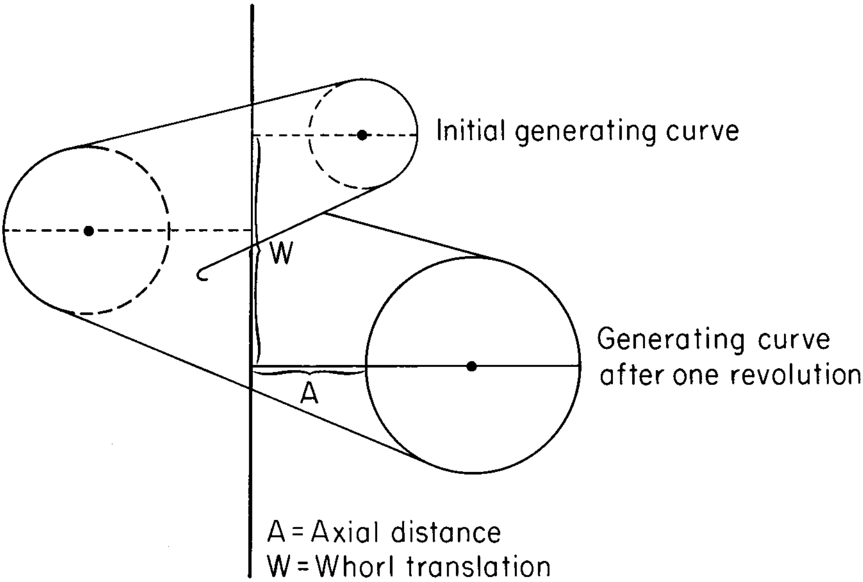


Figure 5.7. Raup's geometrical abstraction of the coiled shell.

3. *Axial distance:* The distance between the generating curve and the axis of coiling
4. *Generating curve angle:* The angle between the geometric and biological generating curves

To simulate a conispiral form, one more rule is required:

5. *Whorl translation rate:* The rate of movement of the generating curve parallel to the coiling axis

This gives us a formal means of understanding the range of variation of a form. But we see immediately that a living or extinct taxon cannot be found for all combinations of these parameters; actual coiled shells of groups such as gastropods and ectocochliate cephalopods occupy only a small part of the conceivable morphospace. Correlations exist between some of the parameters. In gastropods, for example, increasing whorl translation rate is usually correlated with rather low whorl expansion rate. Thus, the common abalone-shaped shells (e.g., *Haliotis*), with high expansion and low translation rates, turbinate shapes with intermediate values, and high-spired forms (e.g., *Turritella*), with high translation and low expansion rates, are common morphotypes (see Linsley 1977). The important question raised by theoretical morphology is: Why is the morphospace not occupied fully?

A sensitivity analysis of deviations from a geometric program may reveal "weak points" where ultimate shape change will change radically, with strong negative consequences for performance (Bayer 1978). Theoretical morphology therefore leads us to forms in which strong stabilizing selection might be in force. For example, a small deviation along the coiling axis can change a planispiral into a helicospiral growth pattern. In contrast, a small deviation in an already helicospiral pattern does not change the shape qualitatively. Such an "error" in a growth program might have important consequences for a cephalopod whose hydrodynamic stability and streamlining depend on the maintenance of the planispiral condition. Such errors would also create great difficulties for bivalves and brachiopods, owing to the necessity of articulating two planispiral valves. Bayer claimed that such errors are more commonly seen in typically helicospiral gastropods than in planispiral shelled cephalopods, and this reflects the presence of a strong regulating system in cephalopods to avoid such errors.

Some studies of gastropod form illustrate the potential power of the theoretical morphological approach in analyzing functional problems. Cain (1977) looked at the overall spectrum of snail shapes, as indicated by spire index (height/maximum shell diameter) ratios. A bimodality in spire index (0.5 and 0.3) is found in many snail faunas. He concluded that this must be due to natural selection, whose action results in two modes of overall shape, each conferring stability to an animal that must carry a house on its back, while often crawling in a water current. Intermediate-spired forms may be at a disadvantage because they cannot easily deploy the shell without having the center of gravity rather high above the point of attachment to the substratum, which creates a torque that slows crawling speed (see Linsley 1977). Lower-spired forms, such as abalones, have the center of gravity near the substratum. Moderately high spired forms can deploy the shell nearer the substratum, as it is possible for the plane of the aperture to converge on the axis of coiling, thus reducing the amount of inclination necessary to maintain a tangential aperture and increasing the amount of detorsion during development (Linsley 1977, and references cited therein). Both these forms are faster than intermediate-spired forms. Thus, where crawling speed is at a premium, one might expect bimodality of form. Very high spired forms, such as *Terebra,* drag the shell along the substratum and are therefore quite slow.

The late Peter Williamson further illuminated this problem by considering constraints that would enhance shell strength, which should be maximized when the whorls touch. This constraint greatly limits the range of overall morphologies. If one sampled this range randomly, one would be likely to get a bimodal set of spire index values, which calls into question Cain's (1977) functional interpretation of bimodality of snail form. This overall conclusion is tentative because entire faunas adhere to one mode of spire index value that can differ from a random sampling of the range predicted by Williamson. Moreover, as mentioned above, crawling speed is maximized at two modes of shape. Owing to the constraint of whorl contact, spire index variation may obtain a range of equally acceptable values. Other factors, however, may cause an animal to have a given length or height, thus setting its form within the overall field. Clearly, the overall story is more complicated. Nevertheless, Williamson's fascinating reinterpretation calls into question any hasty conclusions of completely functional significance for even rather complex multimodal patterns of forms in a group of related taxa.

Thomas and Reif (1993) have considered the issue of theoretical morphology at the grandest scale, which includes the entire range of possible skeletons, the so-called skeleton space (Figure 5.8). Skeletal morphologies can be rendered into the following components:

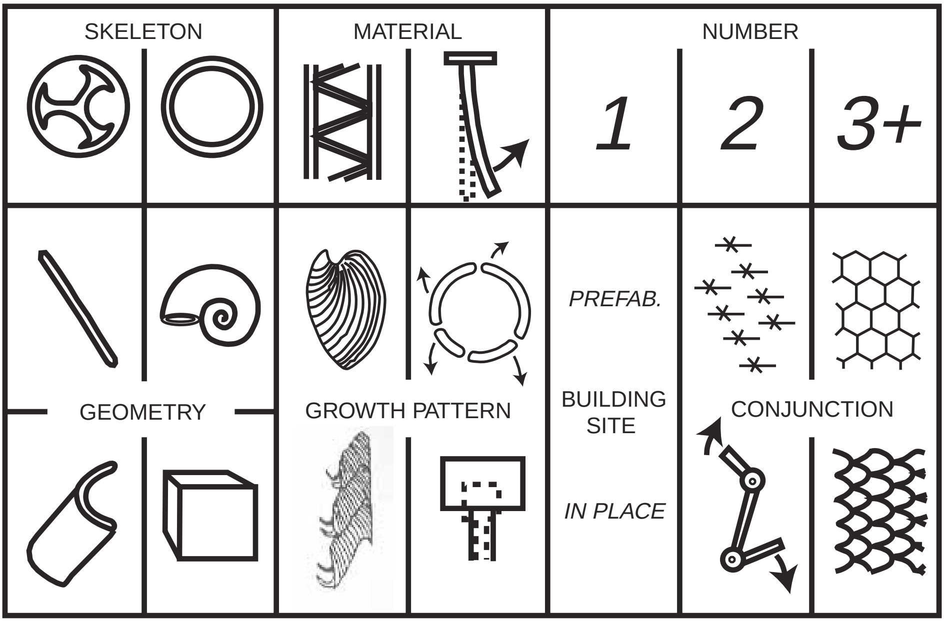


Figure 5.8. Parameters and states of the skeleton space. (Modified from Thomas and Reif 1993.)

1. Internal or external
2. Geometry: rod, sheet, block, coil
3. Material: rigid, flexible
4. Growth pattern: accretionary, addition of units, replacement/molting, reformation
5. Number of units: 1, 2, 3+
6. Conjunction: no contact of skeletal units, jointed, sutured-fused, imbricate
7. Building site: in situ or away

Such a scale creates a new and somewhat unfamiliar landscape. With the skeleton space as a reference point, the arthropods are far less morphologically disparate than vertebrates and mollusks. Overall, animal life has exploited a surprisingly wide range of the space. By the Early Cambrian, 146 of 182 possible two-element combinations were exploited by animals (Thomas, Shearman, and Stewart 2000). About one third of the combinations of the above states are unoccupied by living species. As we shall see below, theoretical morphological analyses can be combined with functional arguments to make predictions about adaptive occupation of morphological space.

Could we ever deduce an optimal form? Although the trilobite lenses studied by Clarkson are apparent examples of functional perfection, optimality criteria cannot usually be deduced in so simple a manner. At least four major problems hamper a pure optimality approach:

1. *Lack of a unique solution owing to phylogenetic eccentricity – different functional–phylogenetic constraints:* We know that organisms perform the same func-

tions in radically different ways. Consider the function *feeding on macroalgae on a wave-exposed shore.* There may be an optimal form for such a function, but we know that many divergent organisms employ entirely different structures to gather, crush, or tear apart food. How does one compare the Aristotle's lantern of sea urchins, for example, with the radular and buccal apparatus of snails? Either we admit that both serve the function well or we are left with the choice of absurd conclusions that (1) one is perfect and therefore the other will eventually be modified in this direction or (2) neither is perfect and both will converge to yet another structure, with further natural selection. The solution to this is obvious. Both serve the function well but have evolved within a unique set of design constraints deriving from different evolutionary histories. The problem would have to be restated as follows: Given a foot, gill, and radula, what morphology should a snail have to consume macroalgae on a wave-exposed rocky shore?

2. *A series of equally suitable solutions:* Even within the same design constraints, the optimal solution may be a series of morphologies, all equally suited to perform the function. A variety of toxic substances might serve equally well in harming a predator, particularly if there is a threshold of toxicity above which the predator will be completely discouraged from trying another attack. Thus, marine organisms employ metals such as vanadium (Stoecker 1978), hormones like prostaglandin (Gerhart 1984), sulfuric acid (Stoecker 1978), and a variety of other compounds. Similarly, a variety of warning colorations and patterns will be equally effective in associating visual stimuli with the bad experience of the poison. Thus, mimicry rings of butterflies converge on the same bright colors, but rings with more than one color or pattern exist in a region and probably are equally effective (Turner 1981).
3. *Differential response to the same microenvironment:* Even when located in the same microenvironment, an organism may determine its own microhabitat, by virtue of its size and shape. This problem arises especially when one selection force (e.g., protruding into the flowing water from the bottom to gather food) encumbers different microenvironmental conditions depending on the selection of a particular subset from the possible set of strategies (e.g., feeding near the bottom with smaller body size as opposed to feeding off of the bottom with larger body size).

The problem of scaling raises difficulties in relating organisms of differing sizes to the same environmental conditions (Koehl 1976). A good example of this problem arises in the attempt to understand the flow regime around an organism. Body size and velocity of flow are both important in determining the nature of flow. The Reynolds number, Re, summarizes flow characteristics about an object and estimates the relative importance of viscous and inertial forces. If U is the water velocity, l is the characteristic length (it may be the diameter of the organism, colony branch, feeding structure, etc.), and v is the kinematic viscosity, then

$$Re = Ul/v$$

As examples, an invertebrate larva, 0.3 millimeters long, moving at 1 millimeter per second, would have a Re of 0.3, whereas a tuna swimming at the same speed would have a Re of 3×10^6. Viscous forces dominate as Re decreases. As Re

increases, however, inertial forces dominate, increasing the potential importance of turbulence. When *Re* exceeds 2,000, flow about the object (organism) usually becomes turbulent. (See Vogel 1981 or Denny 1993 for an excellent introduction.)

A change in flow regime can be seen easily with change in *Re* as water flows past a cylinder (Figure 5.9). At low Reynolds numbers, vortices are absent in the wake of the cylinder. As the *Re* increases, vortices and then full turbulence develop in the wake. Note that *Re* can increase linearly with current velocity *and* cylinder diameter. A variety of organisms of widely varying size, therefore, will have considerably different downstream water flow patterns. The nature of flow downstream from the organism may determine the nature of food capture by passive suspension feeders. In the gorgonian *Leptogorgia,* Leversee (1976) found that brine shrimp could remain in downstream eddies for as long as 15 seconds. Polyps of these colonies could feed on the downstream side of the branch. *Re* was estimated to be about 50. By contrast, eddies at higher *Re* might not be so predictable and food supply might be less reliable for downstream capture. This problem would be of special importance in colonial organisms that made a permanent commitment to feeding structures in the up- or downstream direction of the colony.

The differential microenvironment created about organisms with varying forms cannot always be related to a simple parameter such as *Re.* Organisms in flowing regimes often are constructed of widely varying materials and therefore are constrained to deal with a given flow regime in disparate ways (Koehl 1976; Koehl and Wainwright 1977).

4. *Conflicting selection pressures within the same microenvironment:* Even when the microenvironment can be specified properly, it is not always obvious what selective pressures are presented to the organism. A set of responses that solve one

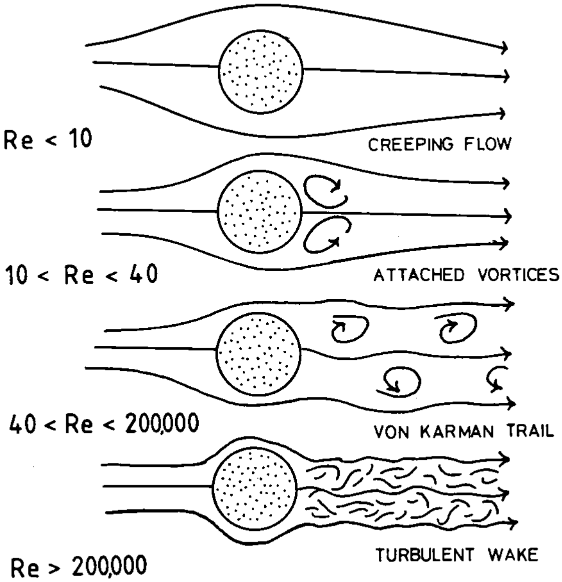


Figure 5.9. Flow patterns perpendicular to the long axis of a cylinder. (After Vogel 1981.)

> problem for the organism may have disadvantages in other autecological dimensions. The paleoautecologist must be able to scale the environment such that these conflicting selective pressures are characterized properly.

Such conflicts can be extracted from our discussion above of sessile colonial organisms in flowing water. To maximize capture of plankton, a stiff fan-shaped structure normal to the current, with feeding individuals on the upstream side, will usually be best. This structure, however, maximizes drag and tensile stress and subjects the colony to the danger of breakage in strong currents. The degree to which an organism solves this tradeoff must be a function of the material of which the organism is constructed and the current velocity.

Constructional morphology. *Constructional morphology,* an approach to functional morphology developed by Adolf Seilacher (1970), integrates the various determinants of morphology into a coherent system, useful for evolutionary and functional considerations. Seilacher defined three principal controls on morphology: (1) *architectural constraints*; (2) *ecological, adaptive, and functional aspects*; (3) *historical–phylogenetic aspects*. Raup (1972a) has added (4) chance and (5) ecophenotypic effects as causes of morphological variation.

Architectural constraints refer to those aspects of an organism, built into its overall biology, that either (1) determine form, irrespective of functional considerations, or (2) modify the evolution of form, interacting with function. Seilacher referred to the first as *fabricational noise*. Certain aspects of form come not from any solution to an environmental problem. They arise rather from the physical principle behind the formation of the structure or from certain biologically controlled processes of formation. The second form of constraint refers to those instances in which such fabricational noise cannot be factored out simply but interacts with functional controls in a complex manner.

To test the hypothesis of fabricational noise, a *constructional paradigm* (Seilacher 1979) is first established, which is used to predict a structure. Theoretical morphology as described above is used to predict one structure or a range of forms. The closeness of match of the structure to the constructional paradigm is thought to be an indication of the efficacy of the fabricational noise hypothesis. Similar patterns found in widely divergent organisms, involved in strongly differing functions, are likely candidates for such fabricational hypotheses. Deviations from the constructional paradigm call for alternative constructional hypotheses or other explanations.

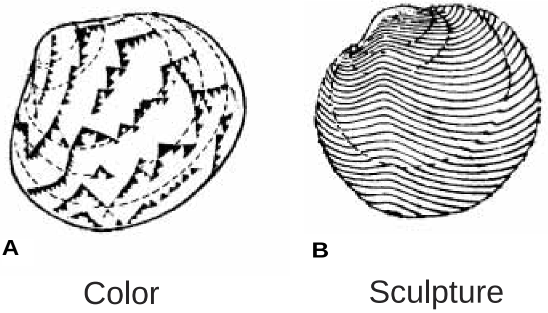
Seilacher (1973, 1979) gave a variety of possible examples of fabricational noise. He likened overall form of urchins and sand dollars to an encrusted liquid-filled balloon, under some gravitational stress. The overall form, therefore, may have various geometric peculiarities that have nothing to do with functional superiority over other possible forms. The surface sculpture of the burrowing mole crab, *Emerita talpoida,* and the detailed suture patterns of some ammonites are claimed to be "pull-off" structures – that is, ridges whose form is determined as the skeletal secretory tissue is finally pulled off from the newly formed and still malleable skeletal material. This is consistent with the discovery of epidermal "feet" – cytoskeletal extensions that participate in deposition of arthropod cuticle; their contractions are known to cause the formation of transverse ripples in the soft cuticle, which later harden (Locke and Huie 1981). Divaricate color patterns and sculpture in bivalves (Figure 5.10) may also be examples of a fabricational contribution to morphology. Both may be controlled by a similar underlying mechanism of material transport and deposition (either pigment or calcium carbonate), but the structures can be employed to serve a function. Divaricate ridges aid in entry into the sediment (Stanley 1970), whereas divaricate color patterns are probably of use in camouflage. In the former case, the pattern seems preadapted for rocking back and forth, whereas burrowing and ridges have been added to permit gripping of the sediment (Stanley 1970). In the case of divaricate color patterns, one can see strong modifications, but it is apparent that many fabricational origins might serve equally well as templates for the patterns.

We should take architectural constraints to be a subset of Seilacher's historical–phylogenetic controls. When a species is confronted with a new environmental challenge and variation is suitable for adaptation, then architectural constraints will channel evolutionary direction, as in the case of divaricate structures mentioned above. In chapter 4, we discussed a variety of developmental processes that are likely to generate fabricational noise. Color patterns generated by diffusion-reaction processes, for example, are liable to take on a finite set of forms, governed not by function but by the geometric features of the reaction field. Developmentally regulated patterns need not be uniquely phylogenetic, however. For example, mammalian coat color patterns, hypothesized to originate in the early embryo (Murray 1981), reflect overall principles that might apply to color patterns in other groups.

Historical differences, to a degree, can be considered separately from phylogenetic controls. A group may have originated or evolved under a unique set of circumstances. This may have led to a set of adaptations unique to that local area. Subsequent movement of the taxon into a very different environment may have resulted in modifications of form, but the stamp of previous circumstances may still be present. This may be because (1) there is present a set of encumbered problems in losing the structure, (2) not enough time has elapsed to lose the structure or no strong loss in performance is involved if the structure is retained, and (3) the structure has been modified to perform other functions but its historical context still is recognizable.

It would be hard to estimate the difficulty of losing a morphological structure in a lineage. In chapter 4, we discussed a variety of developmental justifications for the

Figure 5.10. Divaricate fabricational patterns in bivalves. **(A)** Divaricate color patterns in a bivalve. **(B)** Divaricate sculpture allows flattened and circular bivalves to penetrate the sediment by rocking and using one set of ribs to grip the sediment while the bivalve slides in with the other rib set moving parallel to the sediment.



presence of a *burden* of loss of a structure, based on genetic and developmental pleiotropy. But these can rarely be measured. The issue of time is equally difficult and can be invoked ad hoc to explain the presence of everything from vestigial structures to organs that have been lost partially, such as eyes in fishes living in cave pools. Consider the question of hypotonicity of marine teleost fish, who maintain an osmotic strength one third that of seawater. They must continuously osmoregulate in a medium to which nearly all other marine creatures are approximately isotonic. Some have argued that this reflects the origin of the group in brackish water of a salinity corresponding to the tonicity of fish body fluids. Subsequent osmoregulatory adaptations have been, therefore, superposed on this accident of history. Although this hypothesis may very well be true, it is probably impossible to test.

To analyze a constructional morphology problem properly, it would be necessary to have a tree of evolutionary relationships, to map characters and their change in the taxon in question. A test of the fabrication hypothesis might be fashioned as follows. The fabricational hypothesis would be supported if "fabricational trait" *A* existed in clade I and all species exposed to selective regime *X* showed a changed character state in *A* that resembled the fabricational constraint, but other changes occurred in morphologies where *A* did not exist in clade II. A crucial problem with this test is the demonstration of a selective regime. This can be done only by a convincing case that the traits in the extant taxa evolved under a specific selective regime and no other. Comparative methods can be adapted from those in Table 5.1.

Optimality, adaptation, and constructional morphology. Optimality presumes a fit to the environment in which the organism is found. It is a static concept, independent of history. In contrast, the essence of the concept of adaptation is its historical context. Thus, optimality does not necessarily imply adaptation. The example given above for syrphid flies of a match of form (labellum) to environment (flower corolla) is an example of the difficulty of translating a static situation directly into a historical inference of adaptation. Does optimality therefore imply anything, and is it a useful concept in evolutionary biology?

Optimal foraging theory makes a series of predictions that, when satisfied, carry the connotation of excellent fit of function to environment. But one cannot exclude the possibility that this fit involves a behavioral matching to the appropriate environment, precluding the necessary inference of gradual evolutionary modification to fit the environment. Certain features, however, have built in them an inescapable necessity of adaptation. If, for example, a consumer forages optimally, under a variety of experimental conditions, we must conclude that some evolutionary process has built in a capability to change the rules as new environments are encountered. Some excellent examples of such fits can be found (e.g., see Pyke 1984).

The pure notion of optimality in form or behavior presumes that no genetic, developmental, historical, or other constraints prevent evolutionary progress toward the optimal state. But all that we have learned about evolution belies this extreme claim, which is not seriously believed in any event by most evolutionary biologists.

Lewontin (1978) and Gould and Lewontin (1979) have mounted the most concerted attacks against optimality. To find a function in every structure was supposedly the objective of any "good" Darwinian. Ironically, this faith has usually proven well invested. Anatomical structures, usually thought to be functionless curiosities at first, have often proven to have essential functions. Most biologists have not thought that structures are perfect, only that they do something!

But Gould and Lewontin (1979) point out that history can cast a strong imprint on form, to the degree that we may spend an embarrassing amount of effort trying to prove a functional *superiority* for a structure that has arisen in a nonfunctional context. Lewontin (1978) gave the example of determining the selective significance of the one-horned Indian rhinoceros versus the two-horned African rhinoceros. He claims that a biologist devoted to optimality would try to infer a reason for the difference, when it is likely that it is unrelated to natural selection. As the presence and size of horns may have selective significance (Clutton-Brock and Harvey 1979) and the particular case is uninvestigated, perhaps Lewontin could have picked a better example. Gould and Lewontin (1979) were on somewhat safer ground in using a nonorganismal example, the spandrels of the Basilica of San Marco in Venice, a set of triangular spaces created as a result of the mounting of a dome on a series of rounded arches. The spaces are decorated because they are there. The spandrels were not created for the decorations! Gould (1997) saw spandrels embedded everywhere in the history of life. Maynard Smith's (1979) criteria for satisfying optimality considerations dismantled Gould and Lewontin's apparent belief that all functional evolutionary biology is blown apart by problems of historicity and constructional limitations. An optimality theory requires something to optimize and must include a series of boundary conditions describing the system. Some of these boundary conditions can be described as a series of ancestral character states on a cladogram, relative to the taxon in question. Gould's criticism (e.g., 1980a) of the selectionist's approach to evolution is an inaccurate caricature in that it assumes the unconstrained possible shaping of form to function. Although there may indeed be cases in which such an outlandish assumption cannot be dismissed, most realize that organisms can be made of skin and bone, are constrained to be denser than air, and so on. These constraints must be included in the boundary conditions for an optimality argument, as Rudwick (1964) did explicitly. This approach is similar to the comparative method, often used qualitatively by systematists (e.g., Mayr 1983). It is true that some cases seem like unfettered perfection, especially in foraging theory. It is also true that some unfortunately rationalize poor fits to optimality theories and then invoke other factors. But there is no reason why historical and fabricational constraints cannot be included as conditions in any optimality theory.

Gould and Lewontin have also complained mightily about the rampant use of atomism to explain form in terms of natural selection. "An organism is atomized into traits and these traits are explained as structures optimally designed by natural selection for their functions" (1979, p. 585). To completely, and inaccurately, demolish the adaptationist program, the small minority of workers[2] who believe that gene action can be mapped simply to emergent morphological and behavioral phenotypic

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[2] For example, Richard Dawkins, who, by the way, showed himself (1983) to be not quite the reductionist Gould (1983b) claimed.

Figure 5.11. A decoration filling a spandrel of the cathedral of San Marco in Venice. (Photo by the author.)

traits are often lumped with the more level-headed majority, who believe that genetic and developmental flexibility is very often sufficient to permit the evolution of structures plausible in function and understandable by models of performance.

Many have criticized Gould and Lewontin's architectural competence, but my sense is that this is beside the point.[3] Instead, it is better to point out that their journeyman mastery and use of the concept of spandrels belie their own argument. If any sophomore-level observer (Sorry, guys!) can interpret that the spandrels are decorated within the constraints of space and number, then why can't evolutionary biologists do the same for traits that appear in an evolutionary tree? Gould and Lewontin both are not accustomed to thinking phylogenetically and this cripples their ability to conceive of a means of investigating adaptation within the context of evolutionary history. Figure 5.11 shows one angel in San Marco whose rectangular

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[3] Gould (1997) defended the spandrel metaphor with enthusiasm, but his majority of citations to periodicals like the *New York Review of Books* suggests that the debate is pretty much outside the realm of science and more in the realm of public intellectual "fun." One critic corrected Gould, stating that San Marco has *pendentives,* not spandrels. How appropriate, as *pendentive* sounds like a combination of *pedantic* and *tendentious.*

aspect is clumsily fitted into a triangular space. Any observer can see that a rectangular motif has been wedged sloppily within the triangular space. Evolution is similarly sloppy and interpretable. Too bad that Gould and Lewontin didn't stick to Seilacher's nonmetaphorical concept of fabricational noise, which captures the essence of coopting a structure while also including a mechanistic argument for the generation of real, not metaphorical, spandrels.

The invocation of fabricational noise can be abused much in the same way as optimality arguments. Cowen's (1981) functional study of the camerate crinoid family Melocrinitidae is based on a pattern of arm branching that Seilacher (1979) likened to fabricational noise when found in a sand dollar. But Cowen's analysis demonstrates otherwise. From the Ordovician to the Late Devonian, arm branching becomes more complex and increasingly resembles a theoretical layout of roads for optimal harvesting on a banana plantation. The pattern demands a rigidity of arrangement of transport found in the rigid camerate crinoid crown but not in more flexible crinoids, where arms can be rearranged, depending on current conditions. The optimal solution for the plantation consists of the pattern in Figure 5.12. Here is a functional analogy between crinoid particle handling and banana gathering:

1. Tube feet trapping food – cut banana with machete
2. Pinnule (ciliary) transport – hand-carry baskets
3. Ramule (ciliary) transport – trucks on dirt roads
4. Arm (ciliary) transport – trucks on arterial roads
5. Digestion in calyx – processing plant

Given the historical documentation and conformance to an optimality model, this example satisfies our requirements to infer adaptation.

Evolutionary optimality and theoretical morphology. Constructional morphology provides boundary rules for the development of *restricted optimality arguments,* or *evolutionary optimality.* Consider the primitive state within a clade. We take the biological limitations, both architectural–fabricational and historical, and use them as restrictions within which optimality is calculated. Under this restriction, organisms are not so much perfect as they are the best possible under the boundary con-

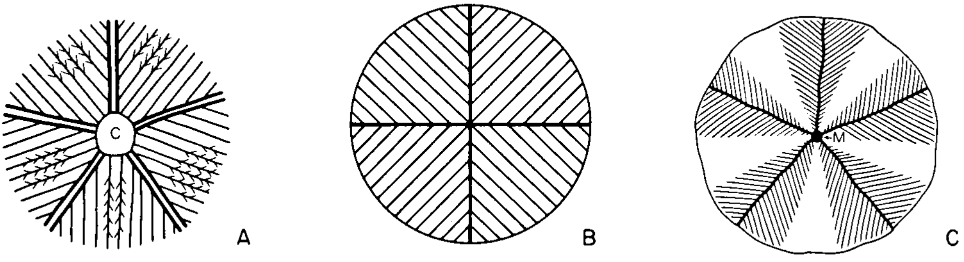

Figure 5.12. Comparison of three gathering schemes; (A) crown of a melocrinitid crinoid; (B) ideal road layout for a banana plantation; (C) food grooves on the sand dollar *Arachnoides.* (After Cowen 1981.)

ditions. I will freely admit that this type of optimality argument invites the danger of rationalization, should an initial pure optimality argument fail to work. Thus, if an organism fails to be an optimal performer, one can invoke a series of phylogenetic limitations. This problem is akin to statistical hypothesis testing, where one has no a priori way of knowing what level of confidence is best and may adjust the threshold level, if an initial attempt to prove significance fails. One must be prepared to make the hypothesis first and be willing to abandon the enterprise if the hypothesis fails. We are not all so courageous.

Theoretical morphology provides an excellent starting point for the study of restricted optimality. A biologically meaningful theoretical generating function is used to produce a range of shapes. Then a set of optimizing principles is used to ask: Within the fabricational limitations of the generating function, what range of shapes would serve a function or functions? This has been a common approach in studies of the coiled shell where the range of shapes of actual organisms is far more restricted than could be generated theoretically (e.g., Chamberlain 1980; McGhee 1980; Raup 1966, 1967).

Ontogenetic change in the form of brachiopods, a dominant Paleozoic (yet still extant) group of marine epibenthic-bivalved animals, illustrates the argument. The animal secretes a pair of external valves that are typically bilaterally symmetrical and articulated along a hinge region. Using a lophophore to gather and sort particles, brachiopods depend on water currents to deliver food to the aperture created by the gaping valves. Each valve grows according to a logarithmic planispiral modified by a successively decreasing whorl expansion rate (McGhee 1980). If there is a correspondence between a developmental process and growth according to the modified logarithmic spiral, then the constructional limitation involves articulating the valves for tight closure. In addition to this constructional constraint, the functional considerations of efficient feeding and stability of the shell in a current should combine to explain the main aspects of overall form.

As has been found for ammonoids (Raup 1967), the biconvex brachiopods occupy a small subset of the conceivable range of geometrical space available to them (McGhee 1980). Very few brachiopod valves have whorl expansion rates of less than 100. This follows the requirement that for distal articulation there can be no whorl overlap between valves. Strong modifications of growth and form at the hinge area satisfy the requirements of hinge articulatory considerations. These limitations of form are related to the limitations of the mode of growth. But form is further restricted according to functional considerations relating to feeding and respiration. One would expect that the animal would maximize the access of outside waters to the internal soft parts, particularly to the lophophore, which is involved in both feeding and oxygen uptake. This is to be expected because the body volume increases with the third power of length, whereas filament area increases only with the second power. Large brachiopods partially offset this geometric limitation by having increasingly convoluted lophophore systems (Rudwick 1970), but one might expect a tendency toward a spherical form, which would give the maximum surface area per unit volume. Because of the limitations on articulation imposed by the growth system, this apex of efficiency cannot be obtained (McGhee 1980, p. 67), but the majority of biconvex brachiopods cluster in the geometric region of minimum internal shell volume–to–shell surface area, given the overall constructional restriction. Such a constructional–functional analysis also tends to highlight outliers, such as the strongly flattened shells of strophomenids and productoids.

Ectocochliate (externally shelled) cephalopods illustrate how constructional morphology can be combined with optimality to produce the evolutionary optimality models necessary to investigate function. Using the parameters mentioned above, Raup (1967) found that coiled fossil cephalopods ranged in shape over a highly restricted range relative to the domain of conceivable shapes. Can this restriction be related to function and to constructional morphology? We presume that buoyancy, balance, strength against implosion, and locomotion, particularly in the special context of jet propulsion characteristic of cephalopods, are functions to be examined most closely.

First we must discuss the limitations of the ectocochliate shell. Cephalopod shells behave like blunt rounded objects moving through a fluid medium. Most of the drag generated relates to a few simple characteristics of the shell: (1) the size of the umbilicus, (2) the width of the shell relative to the diameter, and (3) the aperture size (Chamberlain 1976, 1980). The coefficient of drag (C_D), a linear index of the relative energy required to propel the animal through the water, increases with whorl expansion rate (increasing aperture), increases with distance from the coiling axis (increasing size of umbilicus), and increases as the apertural shape changes from compressed to circular.

The swimming of ectocochliate cephalopods such as *Nautilus* is complicated by the presence of two spatially separated body parts of quite different buoyancy: a mainly gas-filled shell and a soft body-filled terminal chamber. As a result, the center of mass differs from the center of buoyancy. Because the center of buoyancy is usually above the center of mass, the animal has considerable static stability. When fluid is expelled from the hypnome to propel the animal, however, a rocking motion is induced (Figure 5.13). As it moves, *Nautilus* rocks back and forth like a pendulum. The drag exerted by the shell is a minimum of 3 times greater than swimming fishes, mammals, and so forth, and typically 10 times greater. The combination of relatively inefficient jet propulsion, shape, packaging of muscle power, and limitation of rocking during bursts of movement prevents ectocochliates from ever achieving the swimming velocities of fishes, whose center of mass and buoyancy are approximately coincident and whose packaging of muscle power is considerably greater (see literature summarized in Chamberlain 1980).

Ectocochliates were probably nectobenthic in habit, much like the living *Nautilus*. The angelfish are piscine analogues of shape and locomotory habit. This would be in contrast to teardrop shapes (e.g., tuna) that perform sustained swimming or fusiforms (e.g., barracuda or squids) that swim in short rapid bursts. From this, one concludes overall that ectocochliates are shaped and live according to a compromise struck by the inherent limitations of their design and the possibilities offered by the environment.

Are these animals optimally designed to minimize drag, given their overall limitations? Figure 5.14 shows the effect of whorl expansion rate (*W*) and whorl position

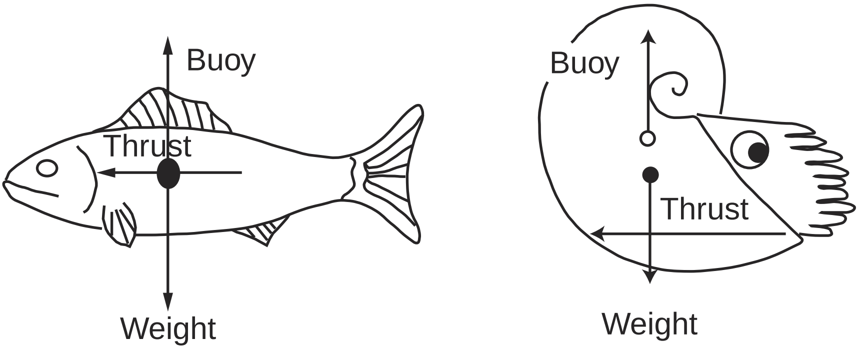

Figure 5.13. Center of buoyancy, balance, and thrust in a typical fish and planispiral shelled cephalopod. Buoy = buoyant force; closed dot = center of mass; open dot = center of buoyancy. (Drawn after Chamberlain 1980.)

(*D*) on the shell drag coefficient of shells with circular cross sections. Drag increases dramatically with increasing *D,* especially as early whorls fail to be obscured by successive whorls. Within the region of relatively low drag, two peaks of minimum drag are apparent, but Figure 5.14 shows that ammonoids of roughly circular cross section mainly fall near one of the peaks. Why this peak and not the other? Apparently because shapes near this peak confer superior static stability. As we have already built in an inherent restriction of swimming efficiency by using a coiled form, the morphology we see is a compromise between, as Chamberlain (1980, p. 325) put it: "the largely antithetical morphological requirements for optimizing static stability and hydrodynamic efficiency." This analysis demonstrates that swimming efficiency and static stability are at least elements in the form variation of coiled cephalopods. One could not perform this analysis without the contributions of theoretical morphology and restricted optimality models, based on biomechanical principles and phylogenetic restrictions.

The overall pattern of cephalopod evolution lacks a trend in relative taxon abundance that can be interpreted as adaptation. Indeed, the dominant Paleozoic nautiloids already fall on the functionally optimal peak. With time, as the nautiloids lose out to the ammonoids, the latter replace the former in modal shape. It is unknown whether this is due to a simple replacement as the nautiloids became extinct, due to an active competitive replacement, or in response to some other factors. It is by no means clear that overall changes in the cephalopod fauna over time had anything at all to do with the swimming efficiency of coexisting taxa. There may be an exception in late Cretaceous times, when a clear increase in swimming efficiency may be related to an increase in predator abundance (Ward 1981). Those lineages without streamlined shells developed sculptures characteristic of predator avoidance (Ward 1981). The question of adaptation in any genus is effectively hidden in smaller-scale historical events that may be beyond the reach of any empirical effort at documentation.

I have discussed a few examples in some detail to show that Gould and Lewontin concocted a straw man argument against a sort of optimality model that is not con-

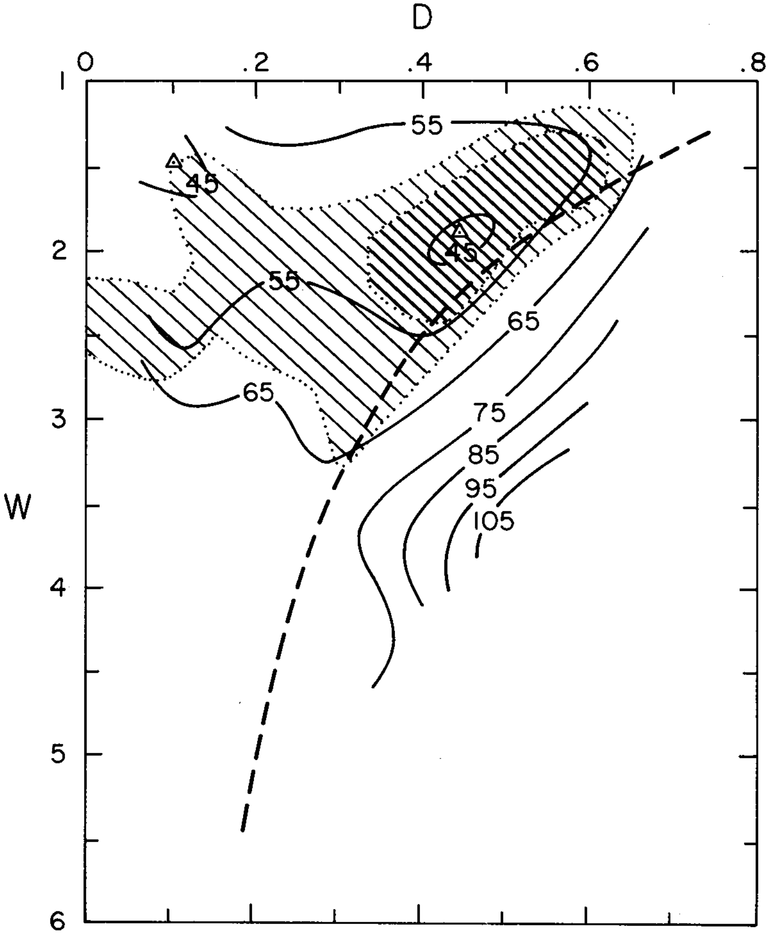

Figure 5.14. Plot of whorl expansion rate *(W)* versus whorl position *(D)* of depressed ammonoids, with contours of the drag coefficient of the shell plotted (lower values indicate lower drag). Dark-shaded area is the range of morphologies of most actual species; light-shaded area indicates total ammonoid domain. (After Chamberlain 1980.)

sidered today by working functional morphologists. Most acknowledge that their evolutionary materials have limitations and seek to formulate optimality models within these limitations. Although Jacob's (1977) metaphor of evolutionary tinkering is a useful way to conceive of evolutionary progress, it is equally clear that the tinkering can be quantified and studied systematically.

Although evolutionary optimality studies are useful in the context of function, they do not illuminate completely the overall question of adaptation. One can formally entertain the hypothesis that the restricted geometric range of form seen in brachiopods may conform with function, but that the morphologies appeared de novo, with no period of modification toward better performance. Alternatively, a large number of more poorly performing taxa may have appeared and become extinct, leaving the residual, which we see in the functionally optimal part of the geometric space. Although I cannot entertain this alternative seriously, it does indicate that the nature of the adaptive process is not solved by constructional optimality arguments. The element of history is absent, except on a grand, and not illuminating, scale, as in the cephalopods. Therefore, to ask in fossil studies, "Does the function suit the structure?," is not necessarily to ask, "Did the structure derive from adaptation?" It is therefore worthwhile to note what *isn't* demonstrated by evolutionary optimality arguments:

1. *Environmental trigger:* Did the environment change and induce a change in form, or did form progressively improve in a constant environment?
2. *Taxonomic level:* Was improvement steadily occurring within evolving lines, or did improvement require selective extinction (Stanley 1975), speciation (Eldredge and Gould 1972; Stanley 1979), or unique types of evolutionary novelties (Goldschmidt 1940, Gould 1980a).
3. *Historical accident:* Did change stem from a unique historical event?

These questions require a record of history and a viable mode of historical inference.

It is rare to be able to find a case in the fossil record where all of these questions can be answered effectively. Most fossil lineages are documented too sparsely and functional morphology is too poorly known to understand the significance of change where relevant. Moreover, the mode of evolution is usually poorly understood (e.g., speciation versus phyletic evolution), as is discussed in chapter 6. Finally, the precision of environmental reconstruction necessary to understand functionally significant changes is usually absent.

An exceptional instance is the evolution of bivalve mollusks, which have an excellent fossil record and can be related functionally to their respective substrata (Stanley 1970). In the Miocene–Pliocene sediments of the mid-Atlantic Coastal Plain, extensive collections have produced a series of well-studied lineages of scallops (e.g., Ward and Blackwelder 1975). The shells of scallops have been studied in detail and the functional significance of variations in the byssal notch, valve symmetry, and the location of adductor muscle scars have been investigated quite successfully (e.g., Stanley 1970). Most interesting is the genus *Chesapecten,* whose evolution and cladistic relationships (see chapter 2), functional morphology, and intraspecies versus interspecies morphological variance have been well studied (Miyazaki and Mickevich 1982).

From the mid-Miocene to the Pliocene (Yorktown formation), the genus shows a continual trend consonant with morphologies departing from byssal attachment and toward increasing commitment to a swimming, free-living mode of life. The variation seen among individuals within a named species is of the same qualitative nature seen between species, so the question of taxonomic level of origin of novelties can be referred to a context easily understood in terms of evolution within populations. Overall, the trend of morphological change seems correlated with a deepening of the near-shore marine basin sediments from which the group is collected. Thus, the evolutionary change can be said to involve adaptation to an environmental change.

Body size trends ought to be explainable, as they are purported to be common enough to be described under Cope's rule, yet they have been usually opaque to causal explanation. Body size could increase over time, supplanting smaller ancestors, but it is also possible for the mean size of descendants to increase simply by adding larger forms to the clade, thus increasing the overall variance of body size. One could not say in such a case that smaller body size is inferior, only that there is some reason that small body size is selected "at the beginning." After the end-Cretaceous extinction, for example, body size of echinoids decreased materially, but this may be a result of selection for very early reproduction at smaller body sizes, owing to a life history shift under conditions of high mortality. Subsequent size increase might reflect merely an addition of species adapted to more stable conditions that reproduce later, live longer, and attain larger body sizes.

Such trends, although often mentioned in textbooks, may be more apparent than real. In the case of Cretaceous mollusks, Jablonski (1997a) has shown that there are no net body size increases over time. In vertebrates, there may be adaptive reasons why increased body size would be selected, but in bivalves and other marine invertebrates, there appears to be no relation between population size and body size, giving no special reason for a size trend over time.

Mammals steadily increased in mean body size through the Tertiary, and this could be related merely to an increase in total size range, following the appearance of diminutive mammals that derived from nocturnal and small Mesozoic ancestors. However, the size trend breaks up into two distinct groups (Alroy 1998): a small-size group that does not change very much, and another group that increases in size with an eventual approach to a size plateau. This may be related to the adaptation of larger mammals to cool and dry conditions that appeared in the later Tertiary. If so, it would be an excellent example of adaptation in the fossil record, across many groups. Certainly, such size increase has been known in mammals for many years, although it was formerly associated with now defunct conceptions of orthogenesis.

Adaptation: Is improvement inevitable and continuous. The use of restricted optimality implies improvement, if by a standard somewhat more restrictive than the optimality criteria that might be concocted in a "from the ground up" design. Is improvement continuous? Are advanced mammals really better than therapsids? Are placentals superior to marsupials? This thinking comes from the pre-Darwinian concept of a *scala naturae,* but it survives in our thinking about adaptation. Although the measure of adaptation must be against an optimal form, the restrictive optimality argument also implies that it must be against a starting set of boundary conditions. If one looks millions of years ahead, it is not obvious that our descendants' performance should be compared with our own. Their measure of improvement must be against their own most immediate descendants.

The potential for lack of overall improvement in performance was demonstrated nicely in a series of experiments for tolerance of yeast to toxic substances (Paquin and Adams 1983). Periodic selection in nonsexual forms resulted in successive sweeps of adaptively superior genes, associated with newly arising mutant clones. Any given clone was found to be superior in resistance only to the previous clone, but not necessarily superior to much earlier clones. This suggests that adaptation has a context: The genotypes that are present in the population at the time the "superior" genotype is favored by selection. In the worst case, overall performance can actually decrease over time.

The performance of complex structures will rarely drift or decrease, so long as the basic organismal structure is about the same. Most improvements in function are liable to be transitive; that is, if improvement *a* is superior to improvement *b,* and *b* is superior to *c,* then *a* will be superior to *c.* An eye with a primitive lens will likely be supplanted by one with a more advanced lens. Such an eye will likely be complemented by complex musculature. These advances are interactive and would likely result in cumulative improvement. Cases of intransitivity are liable to arise when many structures work together to improve overall performance (e.g., to function in a dry milieu), but over millions of years of evolution, a variety of different and functionally and developmentally unrelated structures are co-opted to improve performance. Under these circumstances, one might imagine a taxon achieving dominance by virtue of its impervious skin, whereas a distant descendant might beat its contemporaries by improvements in its metabolic efficiency. Such a complexity of adaptations would not immediately suggest that the first adaptive change resulted in an organism much better in performance than a distant descendant. That is why it is difficult to guess whether mammals are superior over dinosaurs. There is no uniform standard to compare adaptations, even if our prejudices tend to favor fur, mammalian skin, and mammalian metabolism.

The open door to change? Key innovations. We have considered above the analysis of fabricational and functional aspects of form, on the basis of limitations imposed by developmental and architectural constraints and of shapes predicted from functional considerations. But certain evolutionary novelties might bring a form into a new realm of evolutionary potential, permitting a great expansion of form diversity in a group. Such a change may involve (1) a continuous change of a given type of form, past a threshold that has qualitatively different implications for function; (2) acquisition of a new element, which can be readily generated by the available developmental apparatus but whose presence has far-reaching functional significance; or (3) combination of available elements with significance corresponding to item 2. One can also imagine (4) a wholly new structure, appearing as a highly improbable novelty.

Consider a cladogram, complete with character changes registered at the nodes. We might identify a *key innovation* (Hunter 1998; Liem 1973) when the following two criteria are both satisfied:

1. The character change is followed by a large ensemble of other character changes in a set of derived taxa, whose numbers are strikingly larger than the sets of derived taxa following different character changes on other parts of the cladogram.
2. The character change can be shown to have key functional significance in permitting the entire ensemble of derived taxa with their concomitant derived and functionally potent character states, which otherwise are not likely to exist (see Lauder 1981).

In a sense, it is irrelevant how the key innovation was acquired, but one presumes that local circumstances of natural selection, combined with various other constraints and stochastic processes, have yielded a taxon with the change. Thus, the evolution of siphon fusion in bivalve mollusks occurred in a specific environmental context that may not bear any relationship to the ultimate advantage leading to the rise of diverse descendants, which was probably invasion of a wide variety of shifting substrata and protection against predators (Stanley 1968; Vermeij 1983). These local circumstances provide an opportunity but don't guarantee the future of the taxon in question.

The two major criteria for identifying key innovations require an understanding of adaptedness and history. The functional criterion is based on the constructional optimality argument presented above. But history must play a role as well. Conceivably, there is a large ensemble of innovations that functionally might open many new doors to morphological diversity, but one or more historical factors may have prevented their translation into an adaptive radiation. A novelty with great potential, for example, may appear and be fixed in a very small population but will likely disappear. In contrast, the same novelty's appearance in a widespread and populous taxon would ensure its survival and potential to give rise to other changes. A key innovation can have two outcomes: (1) after the key innovation is acquired, the taxon can invade a wide variety of previously extant but unoccupied modes of life (e.g., Lull 1929, p. 246), or (2) after the key innovation is acquired, inferiority of competitors, a change in environment, or extinction of competing forms allows the radiation to occur (e.g., Simpson 1944, p. 193).

The degree of change required to achieve the acquisition of a key novelty in a taxon will vary depending on the overall requirements for functionally significant change, complexity of interactions among parts of the organism, and genetic/developmental mechanisms required for the rise of the novelty. Organismic complexity may allow a wide variety of functionally and developmentally permissible states, thus permitting a smooth transition through many intermediates, of eventually large magnitude (Lauder 1981). In other situations, only slight reconstructions of existing structures permit the change necessary for drastic shifts in habit (Liem 1973).

Key innovations may result from the following evolutionary changes (Galis 1996):

1. *Structural decoupling.* If one structure is forced to serve two functions then evolutionary diversification associated with that structure may be inhibited until decoupling.
2. *New acquisition.* The acquisition of a qualitatively new feature may allow a clade to invade a new and diverse ecological and functional realm.
3. *Loss of function, freeing structure for a new function.* A structure may lose a function, which allows its redeployment for another function that may allow diversification.
4. *Duplication of structures, followed by diversification.* Duplication is one of the most obvious of opportunities for diversification of function. Such origins range from gene duplications to duplications of so-called serially homologous structures.

Jaanusson (1973, 1981) pointed out that many important innovations appear as discontinuous morphological changes. In fossils, the alternative morphs may coexist in a population but are often different enough to be assigned to different taxa. This is true, for example, in graptolites, where coexisting forms with different numbers of stipes are probably temporally transitional polymorphisms from the same species, different to the degree that they have been assigned to different genera (Skevington

1967). As discussed in chapter 3, known genetic and developmental mechanisms easily account for such discontinuities. Nevertheless, some of them may bridge important functional gaps and have great significance for future evolution. Jaanusson (1981) called these *dithyrial* (two-door) populations.

A rather interesting case that lacks the historical requirements for designation as a key innovation (the group bearing the novelty is near extinction and has not given rise to a large variety of derived taxa) is the movable joint present in the maxillary bone of bolyerine snakes of Round Island, near Mauritius (Frazzetta 1970). The acquisition of the joint probably involved a transitional stage in which individuals both bearing and lacking the joint were present in the population. Rather simple genetic–developmental mechanisms would permit the appearance of such a novelty, but its fixation might have led the group toward the evolution of a wide variety of dietary adaptations. The fact that this did not happen raises questions as to the predictive nature of key innovations. Can we explain them only with post hoc just-so stories?

The degree of jaw diversity in several endemic radiations of cichlid fishes in African rift valley lakes may have depended on changes in the pharyngeal jaws and would thus constitute a case of a key innovation (Liem 1973, 1980). As mentioned above, a key innovation is a necessary but not sufficient condition for a radiation in morphological diversity. The particular breeding behavior of the cichlids and the stability of the lake systems may have been the important elements that fostered the radiation. The anatomical changes involve (1) a synarthrosis between lower pharyngeal jaws, (2) a shift of insertion of the two fourth levator external muscles, and (3) the establishment of synovial joints between the upper pharyngeal jaws and the basicranium. These changes decoupled and freed the premaxillary and mandibular jaws to evolve numerous specializations in the collection of diverse foods (Liem 1973).

A primitive neotropical form, *Cichla ocellaris,* has a basipharyngeal joint and lacks a complete synarthrosis in the lower branchial jaw. The fourth levator externus is weakly developed and is usually inserted on the lower jaw. In a few specimens, a part of the muscle is attached to the dorsal aspect of the fourth epibranchial. Both the joint changes and the muscle insertion change require genetically trivial changes.

Petrotilapia tridentiger, a rock scraper with versatile jaw movements, has eight distinct types of jaw movements. On the basis of these movement types, the other African cichlids can be grouped into four overall classes, each with a characteristic subgroup of these types (Liem 1980). These four classes, furthermore, are different overall in feeding behavior (pursuit hunters, ambush hunters, epilithic algal feeders, variable feeders).

Although the key innovation described by Liem may explain the degree of jaw diversity, it may be insufficient to explain the magnitude of speciation of the cichlids in certain lakes. Behavior linked with color recognition may be far more an important explanation of the degree of speciation. The key innovation may have coincidentally permitted some morphological radiation with trophic significance. We do not have a detailed enough tree-based character change analysis to discern between the two hypotheses.

An inspection of evolutionary relationships of cichlids and relatives produces an ambivalent feeling over the importance of key innovations in the large radiations in African rift valley lakes. The sister group of the Cichlidae is not well known, but the cichlids are so speciose that any known candidate is far less diverse (Jensen 1990). There are not many independent instances of the rise of the cichlid jaw syndrome, but a similar set of morphological innovations did arise within the Beloniformes, within which one can find in the Exocoetidea many of the pharyngeal jaw specializations found in the Labridei. The Exocoetidea is more speciose (under 135) than its sister group the Scomberesocoidea (36). But things are a bit more discouraging when looking within the Labridei itself where the adaptation is ubiquitously present. Consider the Embiotocidae, containing only 24 species, as compared to its Pomacentridae (240) plus Labridae (500) sister group. We must invoke additional factors to explain this extreme variation, which is of the same order of magnitude as the Exocoetidea–Scomberesocoidea comparison (Jensen 1990).

We might slip out of this conundrum by arguing that the cichlid pharyngeal jaw syndrome is necessary but not sufficient for a radiation, but what would be the additional factors? It has been argued that sexual selection also is a motor for speciation in cichlids, but some recent evidence from the Mbuna group in Lake Malawi casts some doubt that mate recognition is a driving force in differentiation. Cichlids as a whole are social in nature and display complex behavior, particularly during courtship and spawning. But courtship display by male Mbuna does not appear critical to species recognition. The Mbuna species do not appear to be replete with behavioral innovations. There is no evidence at present to suggest that epigamic sexual selection, acting on courtship behavior, has been a major mechanism in the diversification of the haplochromine species flocks (Mcelroy and Kornfield 1990). The isolation of rock-dwelling Mbuna has also been suggested as a promoter of extensive localized isolation, but the evidence for this is conflicting at present (Moran and Kornfield 1995).

As mentioned above, it is necessary to understand the consequences of a key innovation, and this is difficult to do without an understanding of phylogenetic relationships. Ideally, we would like to examine a sister group of the taxon that acquired the putative key innovation (which is a derived character) and then search for a conspicuous increase in either species richness or correlated evolutionary events in the branch with the key innovation. Unfortunately, the statistical analysis of differential taxon richness on either branch downstream from a node on a tree is far from trivial, especially if there is only one node with two sister groups to be compared (Slowinski and Guyer 1993). Some attempts have been made to search for multiple instances of the rise of a specific derived character. In multiple cases of the rise of a phytophagous insect clade, such clades were found to be more diverse than their nonphytophagous sister groups (Mitter, Farrell, and Wiegmann 1988; Zeh, Zeh, and Smith 1989).

The larger scale consequences of innovations related to insect herbivory are more complex. Labandeira and Sepkoski (1993) found that the major groups of herbivorous insects did not appear to increase in concordance with flowering groups in the Cretaceous. Indeed, these groups were already in place in the Jurassic. But these ancient lineages are associated even in the Recent with preangiosperm seed plants, the conifers and cycads. The phylogenetic ordering of beetle-plant associations of the most ancient types is concordant with the stratigraphic ordering of the insect and plant groups. As it turns out, repeated later origins of angiosperm-feeding individual beetle clades within the Phytophaga are associated with enhanced rates of diversification, suggesting a series of innovation-associated adaptive radiations (Farrell 1998). Farrell was able to contrast five angiosperm-associated groups with sister groups associated with preangiosperm seed plants and found a statistically significant increased diversity of several orders of magnitude in the angiosperm-associated sister groups, totalling about 100,000 species.

We find further strength in the key innovation argument in the evolution of the hypocone, a cusp added to the ancestrally tricuspid (triconodont) upper molar teeth of therian mammals, which evolved polyphyletically in the Cenozoic in over 20 lineages (Hunter and Jernvall 1995). The presence of a hypocone is incompatible with the presence of carnassiform upper molars, as it disrupts occlusal contact between metacrista and paracristid crests that are well developed in carnivorous mammals. Thus, possession of a hypocone is generally thought to be associated with herbivory, as an additional cusp would allow a broader grinding surface. Hypocones arose either as an additional cusp between the protocone and metacone, or outside the triconodont field, as an outgrowth of the cingulum. The hypocone itself appears to be a minor innovation in terms of morphological change, but its association with herbivory has led to extensive diversification in all lineages that adopted it (Figure 5.15).

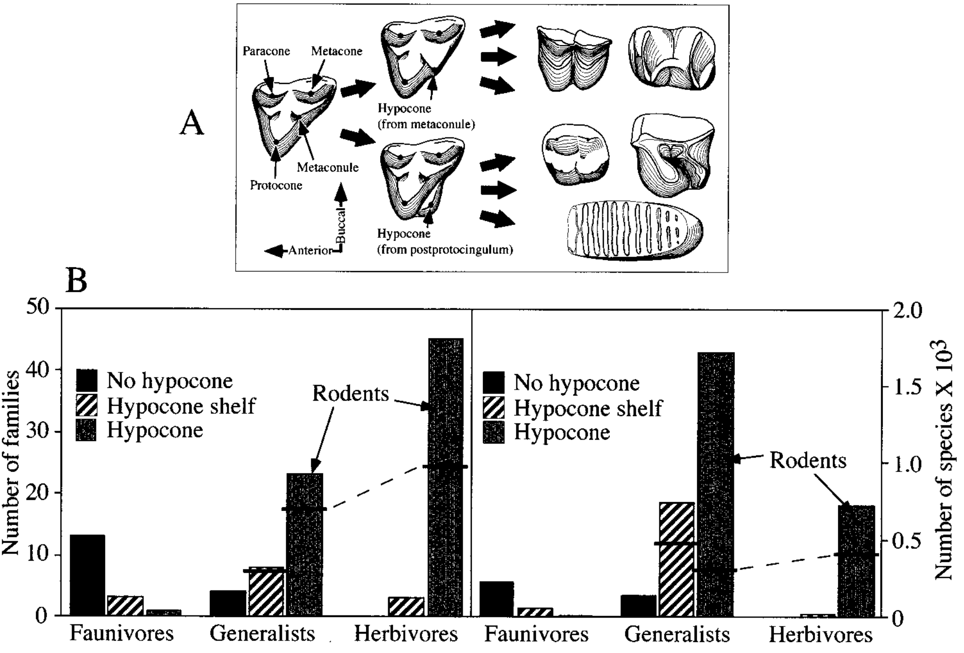

Figure 5.15. Directions and consequences of morphological evolution following the appearance of a hypocone: (A) types of morphological change; (B) family and species-level taxon richness of herbivores and other types with and without hypocones. (After Hunter and Jernvall 1995; © National Academy of Sciences, USA.)

For every nice example such as the mammalian hypocone, we have examples that defy explanation and even embarrass us. If anything is the key innovation for birds, one might think that it would be the presence of feathers, which facilitated the evolution of increased insulation and of flight. But recent discoveries demonstrate that feathers appeared many millions of years, and many evolutionary nodes, before the radiation of flighted birds.

An inverse argument would consider factors that prohibit diversification. Developmental constraints would be obvious characters, especially when they force the retention of couplings between different functions. Werdelin (1987) argued that differences in tooth development between marsupial and placental carnivores demonstrate variations in evolutionary potential. In the Carnivora, the permanent carnassial is preceded by a deciduous carnassial tooth. The permanent tooth can erupt in its geometrically permanent position, and the post-carnassial molars are free to evolve for specialized functions or they can be reduced. In the marsupial Dasyurida, there is relative molar progression, each erupting molar in turn functioning as a carnassial and subsequently being pushed forward in the jaw by the next erupting molar. Thus, all molars have carnassiform morphology and are not as free to evolve into other functions and morphologies. The greater plasticity of Carnivora has led to a diversely occupied adaptive zone, which in turn has led to greater taxonomic diversity within Carnivora than within Dasyurida.

Problems arise, however, when considering evolutionary radiations of groups in which a large complex of morphological, physiological, and biochemical features are apparently involved in the group's success. This is true of groups such as the mammals, where many innovations combined to spell success and whose interactions, for many mammalian features, do not place any particular innovation before another in overall importance in explaining the group's evolutionary success (Kemp 1982). The relationship of single innovations to large morphological complexes reaches a pinnacle of confusion in the use of the term *bauplan.* In McGhee's excellent study of brachiopod form, *bauplan* is used to describe the general growth pattern of a pair of articulated valves, each growing according to a modified logarithmic spiral. This feature alone creates the many constraints used in McGhee's functional model. But Gould (1983b) used the term to apply, for example, to the complex of adaptations that make up the Felidae. This includes a set of mammalian features, plus additional felid synapomorphies. A pussycat sees an ecological challenge in a wholly different way than a clam does! But the reason for this may reside in the possession of a large number of characters. As I will show in chapter 7, such baupläne arose gradually, and the pace and order of acquisition of features might have been partially due to historical accident. I discussed in chapter 4 the similar evidence for the gradual construction of some developmental programs. This gradual construction of a character complex should not be equated with single features that constrain evolution, such as logarithmic spiral growth. I assume that the latter is the result of a fairly simple cellular growth mechanism. The term *bauplan* seems to have been used by Gould as an emblem for all notions of character complexes that constrain future evolution. But this is usually confusing without any historical information or functional, developmental, or genetic details.

The Study of Form

Allometry. The measure and analysis of proportional changes in traits with size change is probably the most commonly employed means of studying form (see Cock 1966; Gould 1966; Huxley 1932). The relationship between two measurements is characterized and comparisons are then made, often with functional hypotheses in mind. We assume that two different homologous points can be located on a set of organisms, as termini for each of the two measurements. With the use of an appropriate technique of statistical association, the following general equation is established to relate the first measurement, X_1, to the second, X_2:

$$X_1bX^k{}_2$$

where b is the *allometric coefficient* and k is the *allometric exponent.* If $k = 1$, then shape, as estimated by the two measurements X_1 and X_2, does not change with increasing size, as estimated by either X_1 or X_2. If the exponent differs from 1, then some change of shape with increasing size must occur. If k departs from 1, then it is more convenient to plot log X_1 versus log X_2. The slope of the linear plot equals k, whereas log b is the intercept. Linear regression can be used, but it must be remembered that an error in X_2 causes a downward bias in the estimate of k.

Five main types of allometric relationships can be established, and these are often confused with one another (Cock 1966):

1. *Static:* Relationships are established among individuals of a population that are all of the same age.
2. *Cross-sectional:* Studies come from a set of individuals each of known, but different, age.
3. *Longitudinal:* Studies take measurements for the same individual at different ages. The exponent k is estimated from measurements taken from a group of such individuals.
4. *Mixed cross-sectional:* Studies take single measurements from a group of individuals of different ages, but no exact criterion exists to measure age.
5. *Finally, interspecific comparisons:* These employ representative values from each of several species. These values should be taken from individuals of similar age, sex, and developmental state.

These different comparisons are not equivalent and usually yield different estimates of k and b. This is especially true in interspecific versus intraspecific estimates. For example, the relationship between facial and cranial length of horses in ontogeny is not equivalent to interspecific differences in fossil horses. The exponent is higher in the phylogenetic series, and the value of b differs as well (Reeve and Murray 1942). In the interspecific case, a change in b may be explained as an evolutionary increase in the size of the facial primordium, which accommodates the coordinated evolution of hypsodont teeth. Usually, estimates of k from static comparisons are smaller than for longitudinal studies. In some interspecific cases, the value of k differs when species are compared at different taxonomic levels. Although brain weight increases with the

0.75 power of body weight for the species of mammals as a whole, the exponent for species within genera drops to 0.5 (Harvey and Bennett 1983). Such comparisons often involve great differences in overall size range, so that different mechanisms may be at work when one is looking over three orders of magnitude in size, as opposed to lower-level taxonomic comparisons that may be done within one order.

Comparisons of the exponent k may be used occasionally to draw conclusions on growth patterns and mechanisms of gene action in intraspecific and interspecific studies. In some breeds of dogs, horses, and pigeons, Darwin (1859) noticed that the young of various breeds more closely resembled each other than did the adults. The young of the tumbler pigeon, however, differed from the young of the wild rock pigeon in almost the exact proportions as did the adults of the two breeds. Similar differences have been recognized subsequently by many geneticists. Sinnott and Dunn's (1935) classic paper on genetics and shape differences in plants revealed shape differences that were established in the embryo, as opposed to others that became more exaggerated with increasing age. In the latter case, therefore, it is possible that the allometry lines will converge with decreasing overall size and age. In the former case, the shape difference is established in a developmental stage previous to the one used in the measurements that are plotted. Here, the allometric exponent may be the same but displaced with a different intercept value of b. It is possible that the shape difference was established in a period of allometric growth in this earlier developmental stage or was achieved in one quantum developmental step.

Although studies often focus on differences in the exponent, k, of the allometric equation, variation may also occur commonly in b, with k being identical for all measured individuals (White and Gould 1965). For example, Kurtén (1954) found that the allometric intercept for trigonid length versus crown length in teeth of badgers, *Meles meles,* changed during the Holocene. Trigonid length decreased, with no ontogenetic change of shape toward the present. The *creeper* gene in fowl probably acts at an early stage of development, probably during morphogenesis. From the seventh day onward, the position of the allometry lines, taken in a longitudinal study, for various skeletal dimensions is altered, but k is unchanged. This is common for other chondodystrophies in vertebrates (see Cock 1966, 1969).

Gould (1972) quantified *White's criterion,* the relative difference in size at which shape on two given allometric regressions is the same. If b_i is the allometric intercept for different regressions, i, then

$$S = b_1/b_2^{(1/1-k)}$$

This estimator was usefully applied to the evolution of the Jurassic oyster *Gryphaea,* whose shape evolution has been the subject of much controversy. In the basal Lias, descendant and larger Gryphaeas can be shown to be geometrically scaled-up models of their smaller ancestors. For descendants (younger), $b = 0.237$, whereas for ancestors, $b = 0.210$. The exponent is 1.766 in both cases. From this, we calculate S to be 1.17. This matches closely the ratio in maximum size between the descendant and ancestral oysters, which is 1.21. In contrast, the evolution of coiling in the later Lias consisted of a series of shifts in allometry lines, which retained the same shape at larger sizes in descendants. Gould argued that an evolutionary increase in size provides the primary impetus for changes in shape, as shells of the same shape become more unstable as they grow larger (Hallam 1968). When the actual increase in size lags White's criterion, evolution proceeds via paedomorphosis. This happens in the later Lias, where the ratio of maximum sizes for latest to earliest Gryphaeas considered is 1.76. But $S = 7.42$. The spinatum shells would have attained the same shape as angulata shells had they grown to be 7.42 times as large, but they are not even twice as large in reality.

The value of the allometric exponent can be predicted in some cases from biomechanical and metabolic principles. Indeed, a quest to establish such grand rules is no less than the holy grail of allometrists. The simplest cases of models of scaling arise from conflicts posed by differential expansion of body parts, stresses, or organismal needs. Consider the differential expansion of bone cross-sectional area (S) and body weight (W), as a function of overall length (L). The following equations are to be expected:

$$S = k_1 L^2,\ W = k_2 L^3$$

Therefore:

$$S/W = (k_1/k_2)\ L^{-1}$$

Thus, cross-sectional area must increase at a slower rate than body weight. This would pose a significant problem for a terrestrial vertebrate of considerable weight. As might be expected, limb cross-sectional area is commonly found to increase relative to body length, with an allometric exponent greater than 1. In other cases, such as trees, the height-to-diameter ratio will continue to increase to a point where elastic buckling under wind stress becomes a problem. McMahon (1973) found that trees do not exceed by more than one fourth a critical buckling height.

Although allometric relationships are still pursued like the holy grail, the problem is that there appears to be more than one identity for the grail! The zeal attached to the quest is only heightened by the belief that a grand functional explanation will emerge from a universal exponent. The grandest of all exponents is 0.75, which can relate body mass to respiration rate. But other relationships, such as aorta and tree trunk diameter, also obey the 0.75 rule, as mentioned just above. Could there be a universal explanation?

West and Brown (1997) argued just that. A fascinating collaboration between mathematicians and ecologists has generated a model that is startling and even elegant in its simplicity, while explaining anything from plant vascular systems to branching of insect trachea. These systems have in common a continual branching, accompanied by a successive reduction in diameter, as if one were going upstream from a main river like the Mississippi and traveling to successively smaller and higher-order tributaries. The model is constrained by the final delivery of nutrients, oxygen, or other dissolved moieties to a receiving area that is one cell in diameter, a size-invariant unit. To supply the entire network, they presume the presence of a space-filling fractal network. The functional constraint involves the minimization of energy required to deliver materials through the system. As higher-order branchings occur, one has more branches of smaller diameter. If cross-sectional area is preserved with successive orders of branching, then a 3:4 power law is expected. Such an arrangement conserves total flux, because cross-sectional area is inversely proportional to flow velocity in a pipe. One must account for a change in flow from tubes of larger diameter to narrow tubes such as capillaries, where viscosity dominates fluid movement. Also, branching cannot be entirely area-conserving in mammalian circulatory systems because blood must slow down to allow solute to diffuse across capillary walls. Such factors, including oxygen transport in mammals, will alter the expected 3:4 power relationship somewhat, but presumably the deviations can be predicted. Most importantly, the model provides an explanation for the role of body size in many physiological and ecological processes.

Like many other allometric scalings (see below) the obedience to the 3:4 rule depends on measurements made over many orders of magnitude of body mass. This immediately begs the question of whether slopes are consistently different at smaller scales of body size and, likely, phylogenetic relationship. This has proven to be the case in other allometric scalings, such as the relationship between brain and body size. If so, one wonders about the whole model in the first place, because efficient distribution of resources should presumably supersede other selective forces. Finally, it is intriguing that this model does succeed in predicting that larger organisms are actually somewhat more efficient in gathering resources than smaller organisms: Does this mean that we have a selective force for increasing body size?

One other difficulty looms over any attempt to find a single magic bullet to solve an allometric relationship. What if two conflicting functional constraints add to determine the allometric exponent? Yes, the study by West and Brown rather elegantly combined a number of factors, but they all more or less served the same objective. A simple example of conflict would be resource allocation. Consider a colonial organism, such as a platelike bryozoan, growing along a surface and forming a circular colony with diameter d. Resources could be allocated to three principal functions: zooids for feeding, zooids for reproduction, and peripheral zooids that produce spikes to deter predation. An interesting constraint occurs with regard to addition of zooids with increasing area, because food might be acquired in proportion to area, a function of d^2, but the number of peripheral zooids increases with the order d. If the cost of maintenance of the zooids were low enough, one could rapidly imagine a surplus of resources, relative to what would be needed to add a set of zooids at the periphery. One "solution" would be to devote resources to reproduction. Armstrong (1983) devised a model of plant growth much along these lines and deduced that the optimal allocation would be 2:3 to growth and 1:3 to reproduction. The exact solution isn't important for us, but it is important that conflicting functions may produce unique solutions of their own.

Such *conflicts of function* extend to more general issues of organismal function. It is quite conceivable that some morphological structures are involved in two demanding functions, making participation in one function encumber a cost that inhibits the other. For example, in lizards, locomotion and ventilation apparently both require contraction by some of the same hypaxial muscles attached to the ribs, which results in a significant conflict: Lizards cannot run and breathe at the same time (Carrier 1991). Mammals and birds independently acquired characters that alleviate this dependence. Perhaps the breakdown of the logjam of such an interdependence is the key to evolutionary innovation.

Conflicting constraints may also extend to synthesis of materials, where there is a zero-sum game in the allocation of resources. Fitting with our expectations just mentioned above, the production of spines by bryozoans that resist predators apparently encumbers a cost sufficient to reduce overall colony growth (Clark and Harvell 1992). Nijhout and Emlen (1998) demonstrated that the allocation of insect resources to one exoskeletal structure led to deficiencies in another, which suggests an impediment to the independent evolution of one structure, relative to others.

Allometry and developmental constraint

> Your nose grows as the rest of you grows because you're all one piece!
>
> – from a song by Mr. Fred Rogers

Huxley (1931, 1932) discussed a possible link between developmental constraint and form and concluded that it may have important implications for the interpretation of form in terms of function and evolutionary trends. If we consider a longitudinal study of shape, the value of the allometric exponent and intercept should be explained partially by mechanisms of gene action and development. If this is so, then trends among taxa may be due to the same genetic and developmental mechanisms. Are size changes in phylogeny simply an extrapolation of ontogeny (Gould, 1977)? To the degree that this is true, any evolutionary trend under the influence of functional differences among phenotypes of different shape must be constrained by developmental–genetic effects. Allometry has, therefore, been a primary battleground where proponents of nonadaptive constraints have argued with supporters of entirely adaptive explanations for shape differences in phylogeny.

An excellent hypothetical example emerged from the work of Huxley (1931) on the relationship between antler size and skull size (or body height) in different species of deer (Cervidae). All of the measurements yield an approximate straight line on a log–log plot. This is true to the degree that the spectacular extinct Irish elk (actually a deer), *Megaceros giganteus,* appears on the plot as a "typical" species (Gould 1974). The question is thus: Is the Irish elk a captive of its unusually large size via a genetic–developmental constraint, or is the overall relationship between antler size and skull size among the species simply regulated by natural selection on overall form, based on some as yet poorly understood biomechanical or other selective constraint? Huxley (1932) argued for the former, though he later seemed to abandon this position (Huxley 1960).

A classic study of evolutionary relative growth in titanotheres (Hersh 1934; Osborn 1929) shows a typical interpretation of interspecific allometric relationships based upon developmental constraints. Using Osborn's data, Hersh found the following, when comparing horn length to skull length: (1) species within a genus, consisting of an ancestor–descendant series, have the same values for *b* (allometric coefficient) and *k* (allometric exponent); (2) genera are distinguished from one another by differences in *b* and *k*; (3) *b* is a decreasing function of *k* as phylogeny proceeds. Hersh (1934, p. 548) noted that

> If we were to suppose that the value of *k* for the relation between horn-length and skull-length, instead of being so unusually high, were more nearly a common value in the neighborhood of 1, then a titanothere with a skull length of 800 mm would possess a horn about 1.5 mm long. Even if *k* should have the quite high value of 2.75, such a specimen would have a horn not longer than about 5 mm, which, considering the broad oval base of the titanothere horn, would most likely fail to be detected as more than a change of contour in the fronto-nasal region of the skull.

He used this to reach conclusions of far-reaching importance: (1) The mammalian organization may have a potential mechanism for horn growth. In many groups, however, the horn does not develop because of the allometric relationship, which reflects a developmental process. Therefore, (2) "…the titanotheres of early Eocene times did not have horns because they were not large enough. As mutations for larger size occurred and were selected … the ontogenetic mechanisms for the production of horns was able to produce first incipient horns, and with the passage of generations horns of progressively increasing size were produced" (Hersh 1934, p. 548). Finally, (3): "…the horns in their incipiency were not directly adaptive. But once the horns had reached a sufficient size to be used as organs of offense and defense, we might reasonably conclude that the animals with larger horns, as a consequence of the presence of horns, were selectively favored at the expense of smaller-horned animals…" (p. 550). At this point, selection for larger horns might drag along a correlated selection for larger body size. Hersh concluded that the process would end when the newborn titanothere had a horn so large that it would damage its mother during birth!

I reproduce this argument in some detail because it illustrates beautifully the concept of *developmental constraint* in evolution, so popular again, half a century later. Hersh and Huxley conceived of evolutionary trends as regulated by developmental programs, to the degree that they might be thrust by a correlated evolutionary change into a new realm that is incidentally adaptively significant.

Can geometrical comparisons be so easily translated into developmental and evolutionary change? If development does constrain proportions within developmentally united blocks, then one should be able to dissect an allometric relationship within a clade and see an overall similarity in trends over great and small taxonomic distances. After all, the constraint hypothesis presumes that development locks in a certain overall pattern of growth. Unfortunately, variation is expectable enough that it would be difficult to quantify the magnitude of a deviation from a given allometric exponent that would be sufficient to falsify the limitation of developmental constraint.

Let us return to the antlers of deer. Is the allometric relationship between body size and antler size a product of a genetic–developmental constraint, or is it shaped by natural selection? Arguments by Gould (1977) and Lewontin (1978) support the former. Small deer, such as the muntjac, have small antler size relative to overall body size. But larger species, such as the reindeer or the well-endowed Irish elk, display proportionally far larger antlers. Clutton-Brock, Albon, and Harvey (1980) demonstrated that large deer species tend to be more polygynous (more females mated per male) than smaller species. Larger species, with proportionally larger antlers, tend to form larger breeding groups than do smaller species. This suggests a role for intermale combat. But there is still a significant allometric relationship between shoulder height and antler length within groups identified for similar overall breeding size. The slope of the within-group relationship is less than the one established when species from all groups are considered together. Among other possible explanations, this may be due to a general overall advantage of larger deer and their antlers in mating success over smaller deer. The developmental constraint hypothesis may also be invoked, but it is surely not a hypothesis that seems any more likely than a number of others.

Gould (1974) produced a mixed message about the Irish elk. On the one hand, the magnificent Irish elk was just an ordinary deer whose antlers were not extraordinarily large by the allometric standards of the cervidae. But Gould was clearly concerned about the antlers' size and shape anyway and argued that the Irish elk could not fight, owing to its large palmate antlers, which were thought to be too cumbersome to use in battle. Part of his conclusion was based on an incorrect reconstruction of the orientation of the skull of the Irish elk during combat, which made the use of the antlers unlikely in butting. He argued that the large antlers were more likely just an intermale signal or mate recognition signal. Such signals are of course widespread in many species, particularly birds, where sexual selection has resulted in conspicuous plumage color that is used as a mate recognition signal. But intermale competition in deer involves an interplay between antlers as ornaments and armaments. All deer fight, irrespective of their size. Although males may spar with no damage, males with similarly sized antlers fight aggressively, and much damage and even death may ensue (Barrette and Vandal 1990). On the one hand, a larger, more elegant rack might cause one male to dominate a more diminutive competitor, but on the other hand, one might expect that there would have to be something behind the mere size of the structure – namely, an ability to fight (Berglund, Bisazza, and Pilastro 1996). This, of course, is an adaptive argument, which Gould implicitly dismissed. Antlers and a deer capable of fighting must back up the signal they project. After all, tired large deer with large antlers may succumb in combat to more diminutive deer that enter the rut later in the season. The antlers are a part of combat ability. Gould's argument is absurd because in effect he stated that a soldier is not a soldier, implying that his or her sword is dysfunctional.

It is quite likely that Irish elks *did* fight, as evidenced from a variety of morphological features (Kitchener 1987). First, Irish elks have tines, or posterior projections used to lock horns with other males. When two male deer approach each other, their heads are bowed, which exposes the rear of the antlers and allows them to grapple by means of the tines (Figure 5.16). It would be strange for the Irish elk to have such tines and not be involved in combat. When the skulls are oriented in a plausible way, the brow tines interlock, as they do for large combative deer species. Kitchener (1987) also noted that antlers of living deer who fight have recrystallized hydroxya-

Figure 5.16. An interpretation of combat posture in the Irish elk. Note the role of the brow tines in preventing injury to the eyes. (After Kitchener 1987.)

patite crystals at the point of impact. Away from the point of impact, the hydroxyapatite *c* axes are randomly arrayed, whereas they are parallel where butting occurs. At the presumed point of impact, the Irish elk hydroxyapatite crystals are aligned. Finally, Kitchener (1985) showed that to maintain a similar breaking strength with increasing size, horn basal area should be related to the fourth power of the cross-sectional diameter. The Irish elk conforms to this (as do other deer and sheep), suggesting that its antlers are designed to maintain strength, presumably for combat. The evidence thus suggests that function guides allometry.

In some instances, trends among closely related species seem to cross the overall allometric trend. Such cases, when explained in ecological terms, would appear to falsify the developmental constraint hypothesis. In the primates, testis weight follows an overall allometric relationship with body weight. Significant deviations occur, however, from the overall trend. These can be related to breeding system (Harcourt, Harvey, Larson, and Short 1981). Males of monogamous and harem genera have a smaller testis than those of genera in which several males compete for the same female. In the latter case, the contribution of greater volumes of sperm is selectively advantageous, as it dilutes the chances of contributions from matings by other males. Species with larger testes also have a proportionally larger volume of seminiferous tubules, as opposed to merely increased supportive tissue. The relationship cuts across taxonomic borders. These results suggest that there is an adaptive reason for an overall correlation between body size and testis size but that species-specific differences have selected for significant deviations from the overall trend.

A similar case can be made for deviations from the overall brain size–to–body size allometric relationship found in small mammals and primates. Folivores tend to have smaller brains relative to body weight than do frugivores (Harvey and Bennett

1983). This may be related to the more elaborate ensemble of behaviors required to locate dispersed and clumped sources of fruit, as opposed to more homogeneously distributed leaves. The trends seem to cross freely the overall allometric relationship, suggesting that developmental constraints cannot be that strong. Indeed, the breakdown of such overall allometric curves into distinct and virtually nonoverlapping subgroups suggests that the impressive linearity of larger-scale groupings is deceiving. The primates have notably larger brains for their body weights, which further suggests that the allometric relationship is not frozen by an overall developmental program (Lande 1979b). The relatively small brain relative to body weight of the gorilla (*Gorilla gorilla*) results probably from its folivorous habits, as opposed to the brainily endowed and frugivorous chimpanzee, *Pan troglodytes* (e.g., Harvey and Bennett 1983). In other cases, however, such a prediction does not hold well. On the basis of such reasoning, carnivores would be expected to have larger brains for their body sizes than would ungulates, but this is not the case (Radinsky 1978). The overall slope for all species may have other selective explanations but may have some developmental restrictions as well.

The problem of the overall relationship of brain weight to body weight in mammals has been a subject of controversy, even over the value of the exponent. On the basis of most evidence, the value of the exponent, when comparing all species, is 0.75 (Martin 1981). This suggests the possibility of a relationship with metabolic rate, which also scales on body weight with the same exponent. It is possible that the brain acts as a coordinator of bodily activity correlated with overall metabolic rate.

Allometric exponents relating brain to body size among species at different taxonomic levels often differ. It is the usual case that the value of the exponent, comparing a given measurement with overall body size, decreases as the species compared come from lower taxonomic levels (Clutton-Brock and Harvey 1979; Gould 1975). This has been investigated by Harvey and Bennett (1983). The relationship cannot be easily explained with either a selectionist or developmental constraint hypothesis. If some singular selective or developmental factor tightly regulated the relationship, then the exponent should not differ with taxonomic level. Lande (1979b) and Harvey and Bennett (1983) related this to a difference in rate of response of brain size and body size in the same evolutionary series. If body size responds more rapidly than brain size in an overall trend of size increase, then we would expect a lag time until brain size adjusts to the overall scaling value.

The best possibility of learning the role of genetic and developmental constraints on form would involve a detailed genetic analysis of correlated characters during development and under natural selection. Correlations among characters have both nongenetic and genetic components, and strong intercharacter correlations do not necessarily imply that the two characters are controlled jointly by the same genes (e.g., Atchley and Rutledge 1980; Cock 1969; Sinnott and Dunn 1935). The overall phenotypic correlations among traits can be small because both traits have low heritability and because phenotypic and genotypic correlations are of opposite sign (Atchley and Rutledge 1980).

If we accept a simple model of transmission, with effects on traits explained only by allelic differences, then the response of a trait to selection is

$$D_1 = h_1^2/s_1$$

where D_1 is the change in mean of the trait 1 in a population over one generation, h_1^2 is its heritability, and s_1 the selection differential. The correlated response for trait 2, D_2, during one generation of selection on the first trait is $\gamma_{12}\sigma2\sigma1$, where γ_{12} is the correlation of the additive genetic values of the two traits (Falconer 1981; Lande 1979b for assumptions). Cheverud, Rutledge, and Atchley (1983) studied the quantitative genetics of age-specific trait values in the mouse and found that ontogenetic gene effects most commonly caused an individual to be larger or smaller throughout ontogeny. It was much less common to find genetic effects that were opposite at different ontogenetic stages or to find effects unique to a given stage.

Lande (1979b) used the literature on genetic correlations between brain weight and body weight to conclude that short-term selection experiments would involve mostly change in overall body size, with changes in brain size largely a genetically correlated response. The allometric relationships of closely related species and populations within a species suggest that the genetic regression of brain on body size permits a successful prediction of the magnitude of the brain response when size is increased either by selection or genetic drift. Lande concluded, if the laboratory data are extrapolated to longer-term evolution, that during the long-term allometric diversification within most mammalian orders, there has been more net directional selection of brain size than of body size.

The genetic correlation between brain and body size may vary, depending on the ontogenetic stage on which selection acts (see Atchley 1984a, 1984b). The genetic correlation between brain size and body size is far higher in early postnatal growth in mice than in later growth (Atchley, Riska, Kohn, Plummer, and Rutledge 1984). The genetic correlation between brain size and body size decreases in mice as brain size growth in mice slows and eventually stops. Riska and Atchley (1985) suggested that this ontogenetic change in correlation may explain the increased value of the allometric exponent with increasing level of taxonomic comparison mentioned above. Body size evolution among higher taxa may include rapid shifts involving selection on earlier stages of growth that share more genetic growth determinants with brain size. Evolution among closely related species may involve adjustments of body size, which can be accomplished by selection on genetic components influencing later growth. Although this is an attractive hypothesis, the predicted allometric slope from selection on the earlier stages of growth can range from 0.43 to 0.76, using an estimate of one standard error. Unfortunately, this range embraces the slopes seen among all taxa (0.75) and those observed among more closely related taxa (0.4 and up; Harvey and Martin, unpublished data). The analysis, therefore, may suggest that pleiotropy is indeed important as an evolutionary constraint. It does not prove, however, that the overall brain size–body size relationship is frozen by a long-standing genetic correlation that cannot be overcome. Riska and Atchley interpreted the gorilla's large body size relative to brain size (Martin 1981) as a continuation of later postnatal growth relative to the chimp, whose relative brain size is considerably greater (see also Shea 1983). If the chimp were the ancestor of the gorilla, this reasoning might be justified, but the phylogenetic relationships of these two forms is in hot dispute, and one is certainly not the ancestor of the other. The fact that in such closely related forms body size can change so much relative to brain size suggests a degree of evolutionary lability that would permit fine adjustments of brain to body size to satisfy functional considerations. Moreover, it is not always possible to predict genetic correlations on the basis of developmental expectations. In the fowl, no genetic correlation exists between length of the tarsometacarpus and carpometacarpus, despite the serial homology (Cock 1969). Intercorrelations among skeletal elements are often difficult to understand and impossible to predict (Cock 1969; Cheverud et al. 1983).

The extension of laboratory measurements of genetic correlations among traits to interpretations of field distributions and even interspecific studies is tenuous at best. In *Drosophila,* extrapolations from laboratory measurements are possible to a degree (Robertson 1962). Lines of *D. melanogaster* selected for change in wing, leg, and thorax length showed genetic correlations between wing and leg but not between either and thorax length. In *D. subobscura* and *D. robusta* geographic races, wing length and leg length tend to covary, whereas head width and thorax length do not. The similarities in experiments and geographic variation may be due to genetic mechanisms whose effects are translated through developmental apparatus of the imaginal discs.

Cheverud, Dow, and Leutenegger (1985) suggested an interesting approach to partition phylogenetic constraints from other factors. Total variation in trait values among a group of related species can be divided in a phylogenetic component of the variation, owing to inheritance from an ancestral species, and a residual, which may be explained by other factors. This approach showed that 50% of the variation in sexual dimorphism in weight is due to "phylogeny." Size and diet may account for the residual. One cannot imply from this, however, that the size difference that permeates the whole lineage is due to a developmental constraint. After all, the difference in size between sexes might be strongly constrained by sexual selection or natural selection, which might have been completed before the stem species of the group gave rise to the descendants used in the analysis. If an ancestral species had two eyes and all descendants had the same number, it would be reasonable to hypothesize that there was no genetic variance available for adaptive change, but it would be invalid to claim that the presence of two eyes arose for nonadaptive reasons. It seems Cheverud et al. fell into this trap. It is also possible, however, that a high genetic correlation between the sexes might constrain the response to selection on dimorphism; this would create a sort of inertia (Cheverud et al. 1985). Therefore, Cheverud et al.'s analysis certainly calls for further inspection of the dimorphism.

In conclusion, the available evidence is firm enough to cast considerable doubt on the developmental constraint hypothesis as an explanation for allometric relationships in form. Although no one would doubt that developmental constraints must have a strong influence on short-term selective processes, it seems likely that most of these constraints are breachable over the long term. The intriguing evidence presented by Riska and Atchley may, however, lend credence to a hypothesis of constraint through pleiotropy, but much more information is required before a quantitative assessment can be made.

It is worthwhile to come back to the famous study by Hersh on titanotheres. McKinney and Schoch (1985) reanalyzed his data and found that extrapolative growth along a constant allometric trend does *not* account for the trend of body size and horn size increase (part of this was recognized by Hersh). One requires shifts in the allometric intercept and possible changes in the slope. These may be adaptive responses to more massive body shape, which might increase the stress applied to the horns. This suggests a reversal of the prejudice cited by Gould and Lewontin (1979); Hersh believed in developmental constraints and perhaps saw them when they weren't present! Hersh (1934) apparently exaggerated the allometric slope by over 80%, probably to ensure that a modest change in size would produce a disproportionately large increase in horn size. McKinney and Schoch suggested that this was done to counter the vitalist streak that was common in evolutionary biology at the time. Oddly enough, a belief in a developmental constraint was used to bolster neo-Darwinism!

Other approaches to the comparisons of forms

Form deformations and transformations. Despite the difficulties of establishing ancestors in complex clades, some investigators have been interested in formal analyses of the geometric deformation required to transform one related form into another. D'Arcy Thompson (1915) suggested the method of grid deformation, which placed a rectangular coordinate grid on one species and showed the transformation to a related form by a regular deformation of the grid. This technique is pictorially illuminating and is useful in convincing one that many organisms are related by fairly simple transformations of dimensional proportions. Unlike comparisons, such as bivariate allometry, it gives a comprehensive picture of the entire deformation of form. Its disadvantage, however, lies in its inability to report the deformation quantitatively and its limited applicability to most form deformations, which are far more heterogeneous than can be represented by simple grid deformation (Benson and Chapman 1982; Bookstein 1982). The deformation of a grid is also misleading in that it presumes a set of equally plausible morphologies along the deformation trend, whereas intermediates may often be functionally, genetically, or developmentally implausible.

Recently, several suggestions have been made for the quantitative analyses of transformations between forms via the analysis of *deformation.* An important aspect of these methods is the establishment of *homologous points,* or *h-points* (Siegel and Benson 1982), on both forms. The deformation to be depicted, therefore, has at least a phylogenetic, if not an ancestor–descendant, aspect. The deformation analysis estimates transformation by the degree of displacement of the points. As is well known, the establishment of such h-points can be highly speculative. For example, it would be commonly supposed that the pseudangular process of the cynodonts (advanced mammal like reptiles and probable ancestral group of the mammals) is a point homologous to the angle of the mammalian dentary. Fossil evidence, however, suggests that the mammalian structure is newly derived, independent of the pseudangular process (Jenkins et al. 1983).

Resistant fit theta rho analysis. Resistant fit theta rho analysis (RFTRA) attempts to highlight local form changes by calculating an overall scale for transformation, based on those areas that have not changed very much. First, a series of homologous points is digitized for each form. Then the forms are adjusted to be the same overall size by calculating a scale factor, based on all proportional changes calculated from relative distances between the h-points. To do this, a matrix of values is calculated corresponding to proportionate distances between all h-points on the two figures. For a distance from one h-point to any other, the median proportional change between forms is selected. Eventually, as many medians are produced as there are h-points. Then the median of these medians is used as the scale factor to convert one form to another. The angle needed to rotate the figure to fit the other is estimated with the same repeated medians procedure.

The scale and rotation factors thus obtained are used to multiply the first figure, and this transformation is superposed on the second. Lines are drawn between the proportionally scaled and changed h-points from the transformed first figure and those of the second figure. The angle and distance of these lines is an estimate of the degree of shape change. The RFTRA technique emphasizes those parts where major shape changes have occurred.

Figure 5.17 shows the technique as applied to shape change between males and females of the ostracode *Costa edwardsii.* Note the posterior inflation of the male that is emphasized relative to the remainder of the form, which does not change in shape very much. This comparison shows an essential aspect of the technique: Although it attempts to estimate deformation, it uses two descriptions θ and ρ, more as a convenience to arrive at a deformation estimate that emphasizes locations on the form where contrasts in shape are the greatest. No attempt is made to think of the deformation in terms of a continuously deformed grid, as in the Thompson approach.

Bookstein's *biorthogonal analysis* produces an estimate of deformation that is much closer to the D'Arcy Thompson approach. The major components of strain that produce the change from one form to another are described in terms of two principal orthogonal deformation axes, describing maximal and minimal strain, and defined throughout the form at h-points (Bookstein 1978, 1980). This technique can also be used to calculate summary descriptors of change of populations of h-points

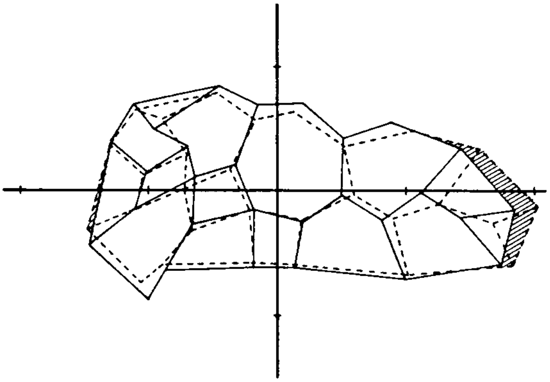

Figure 5.17. The application of resistant fit theta rho analysis to a comparison of a male and a female of the ostracode *Costa edwardsii.* The shaded area indicates the inflation coincident with the larger genitalia of the male. (After Benson and Chapman 1982.)

where shape change is approximately the same (Bookstein 1982). This technique takes better advantage than the RFTRA technique of the available information from the form and shows deformation in far greater local detail (e.g., Figure 5.18). The benefit of more detailed knowledge is balanced by the disadvantage of a large amount of information needed to visualize change.

Simplifying form change into synthetic variables. Direct measures of deformation seem to be by far the most intuitively revealing estimators of form differences between related taxa. The techniques described above, however, are recent developments, and such approaches have been given relatively little attention aside from the common citation of Thompson's famous grids. Form differences have been much more commonly estimated by calculating synthetic variables that either attempt to get the essence of form variation or attempt to recalculate axes along the greatest multivariate directions of form variance. Multivariate morphometric techniques seem to dominate morphometry today (see Blackith and Reyment 1971; Bookstein 1982).

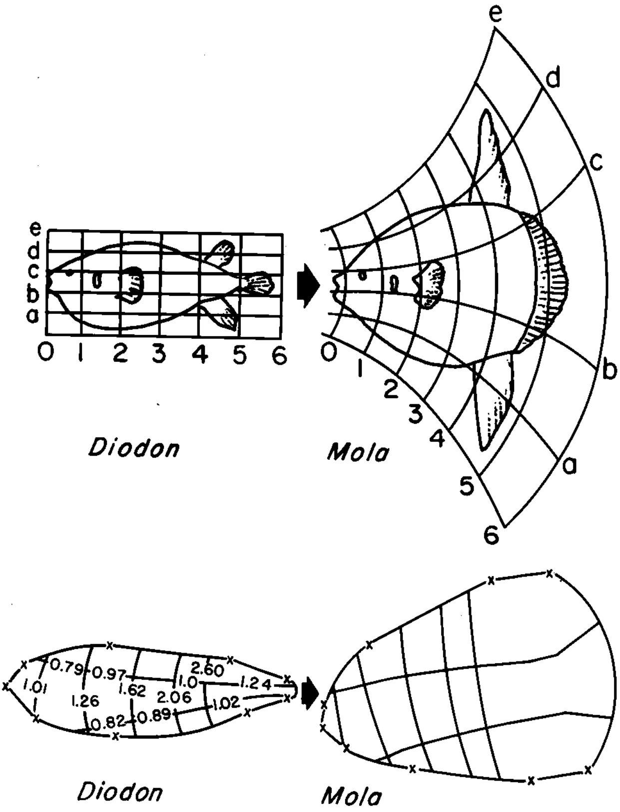

Figure 5.18. Deformation analysis of the transformation of shape between two tetraodontiform fish. Top pair shows change from *Diodon* to *Mola* using the qualitative grid of Thompson. Lower pair shows use of biorthogonal analysis, where numbers on grid for *Diodon* indicate relative stains to produce *Mola*'s form. (After Bookstein et al. 1985.)

A simple technique that illustrates this approach is *fourier analysis* of closed figures, such as the outline trace of a bivalve mollusk. Every location on the periphery of a closed figure can be assigned a vectorial angle and distance, relative to a center point. The overall form can then be described by the sum of a number of cosine functions of varying amplitudes and periodicities (see Kaesler and Waters 1972; see also Brande 1979, for paleontological applications). The meaning of the variables is usually obscure and typically has no direct correspondence to any growth mechanism. Lohman (1983) developed a technique called *eigenshape analysis,* which resolves shape variation into a series of eigenshapes. The first eigenshape accounts for most shape variation and can be used to describe form variation among taxa (e.g., Malmgren, Berggren, and Lohman 1983).

More commonly, *multivariate morphometrics* is used to take a large number of measurements and simplify the overall variation into a variation along a smaller number of dimensions that best describe the variation. *Principal components analysis* (PCA) will serve as an example. (The reader should consult Blackith and Reyment 1971 or Neff and Marcus 1980 for excellent and relatively nontechnical discussions of many techniques.) If *n* measurements are taken on *x* organisms, the *x* organisms can be as a cloud of points (each being an organism) plotted in the multidimensional space. With two dimensions only, and a normal distribution for data, the cloud would take the form of an ellipse. PCA attempts to fit a set of orthogonal axes that run parallel to the major axes of the cloud. In the case of two dimensions, the new axes would be the two principal axes of the ellipse. A given point can then be replotted in terms of the new axes, which maximize the ability to visualize the variance of the overall data set. A principal component of a data matrix is a new variable produced from the linear combinations of the original variables, using the elements of eigenvectors determined from the variance–covariance matrix (Neff and Marcus 1980).

A typical result is as follows. Variation along the first principal component (new axis, if you will) corresponds to variation of body size among the organisms. Variation along the second corresponds to variation in shape (Blackith and Reyment 1971). One can immediately see that the subject of allometry – the change of shape with overall size – can be obscured by the recalculation of these synthetic variables. Also, different means of coding (e.g., mean-centering, normalizing standard deviations to unity) can result in very different results (Neff and Marcus 1980, p. 53). The technique, if used judiciously, can identify covarying characters and thereby reduce the overall need for many measurements. It might also identify a series of measurements whose covariation may have developmental or functional significance. For example, in a study of a hemipteran, Blackith, Davies, and Moy (1963) were able to define fields of form covariation, in terms of molt and body region (Figure 5.19). An allometric enhancement of the mesothorax was definable and is easily related to its specialized role in adult flight. Similarly, the enhancement of the posterior abdomen in the last molt is associated with sexual maturation.

Like most multivariate approaches, the technique is not designed to test a model of form change, nor is it explicitly designed to provide a simple mapping between form change and the final PCA plot. For example, differences in form that are functionally significant may find expression in cases where among-organism variation is

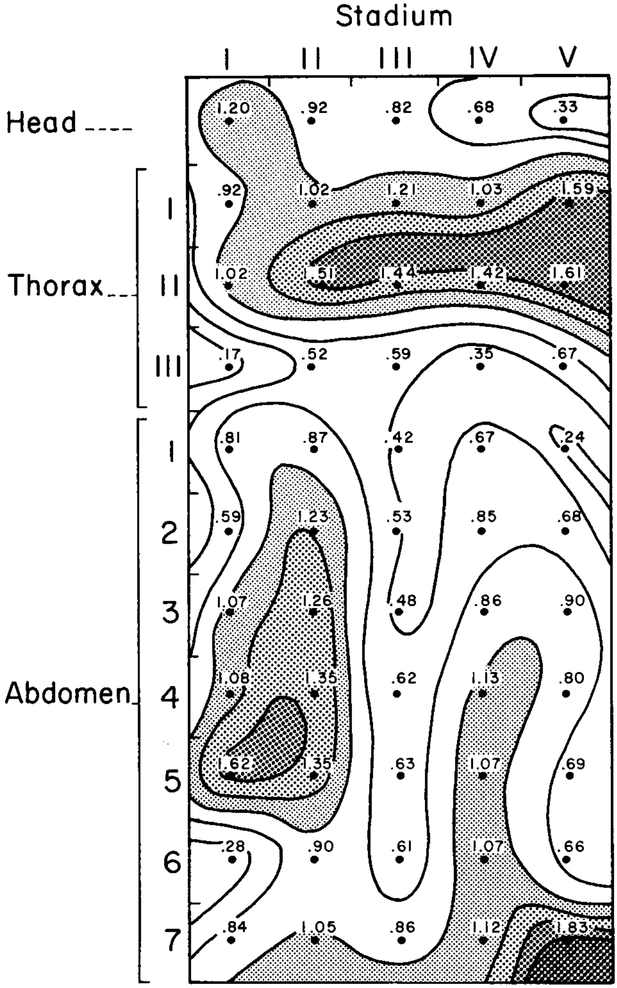

Figure 5.19. Contours of *k* of the allometric equation, for the hemipteran *Dysdercus fasciatus,* relating length of a given part to the total body length, as development proceeds. Darker shading indicates higher values of *k*. Segments and developmental stages are numbered. (After Blackith et al. 1963.)

rather low in magnitude, relative to other more variable and less important traits. Thus, a functionally important difference may be found pressed most heavily along the fourth principal component and therefore will tend to be ignored. Furthermore, a complex form change may be broken up into components that are not geometrically interpretable. If a part of the body is deformed from one organism to the next, it is entirely conceivable that variable elements will plot on one principal component axis, whereas less variable elements will plot on others, even though they are part of the same region of the organism.

In summary, synthetic variables, particularly the ones obtainable in multivariate morphometric approaches, can often be profitably used to interpret among forms.

As most techniques have varying outcomes depending on sometimes overlooked differences (e.g., using a correlation matrix versus a variance–covariance matrix). But, commonly, the relationship between form variation and the new synthetic variables is difficult to establish and may even obscure the discovery of variation in form.

Geometric morphometrics. In a way, you can visualize geometric morphometrics as an extension of biorthogonal analysis. It gives us a means of measuring shape change, even in localized portions of the overall form, with the tremendous advantage of an additional ability to perform statistical analyses and to define the shape change more clearly. Geometric morphometrics is a means of comparing the forms of a group of specimens and defining the parts of the form that differ among specimens. A form is defined by a series of p landmarks, which must be located unambiguously on every specimen. In a phylogenetic context, we would hope the locations to be homologous among specimens. Each landmark has k coordinates ($k = 3$ for three-dimensional space).

If one compares two forms, it is desirable to understand shape differences, but the forms will be of different overall size and the forms will be rotated and translated in space, relative to each other. It is therefore necessary to scale the two forms to a unit size and to rotate and translate the forms in space until one minimizes the distances between landmarks, effecting a sort of maximal superposition (Rohlf 1996, 1999). The methods establishing these distances produces a so-called *shape space,* which is non-Euclidean and therefore not amenable to statistical analyses based on linear differences. To proceed, points in the shape space are projected onto a *tangent space.* One can visualize this by imagining points on a surface of a sphere (shape space) being projected onto a plane (tangent space) tangential to the sphere. The point of contact is a *reference configuration,* which is a mean of all of the specimens, whose distances from each other are established in the shape space by using a technique such as Procrustes analysis (Rohlf and Slice 1990). All of the points on the shape space must be projected onto the tangent space. Specimens that are close together in tangent space are more similar in form. As one moves away from the reference configuration point where the plane meets the sphere, there is more and more difference between the shape space and the tangent space, so one must be careful about using shapes that are very different from each other, as the projection becomes more and more nonlinear among forms (Bookstein 1991). In reality, this is not much of a problem; selection of difference reference configurations gives sets of points in the tangent space that are highly correlated.

Using the reference configuration, each specimen can be described in the tangent space in terms of a component of overall (affine) deformation and local deformations (Rohlf and Marcus 1993). *Partial warp analysis* finds the *thin-plate spline* transformations that map a reference configuration of landmarks onto each specimen. In two dimensions, one can think of thin-plate splines as a function that describes the difference between one shape and another.[4] The partial warps are simple weighted linear combinations of the differences of the specimens from the reference configuration

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[4] This derives from rendering a specimen's difference from the reference configuration as a bending of a metal plate on which the landmarks are plotted.

and are not statistically independent of each other, but they can be used as variables in multivariate statistical analyses such as principal component analysis. Thus, it is now possible to describe shape change in terms of new statistically independent axes using standard multivariate analysis and to perform analyses that involve typical statistical tests, because repeated measures of a given landmark are expected to have, in two dimensions, a bivariate normal distribution of deviations.

If you wanted to perform a phylogenetic analysis, geometric morphometrics suddenly becomes very murky. If you want to score characters in order to construct a tree, what should you do? This is by no means clear as yet. Most of the overall form descriptors we have mentioned above are clearly difficult to use, because there are no homologous characters to compare (Bookstein 1994; Rohlf 1998; Zelditch, Fink, and Swiderski 1995). Geometric morphometrics does have the possible advantage of landmarks that mark the location of possibly homologous locations in a form. But how do we map the form differences between taxa to an evolutionary tree?

Partial warp scores, parameters that are gathered in a morphometric calculation, are continuous characters and are therefore not traditionally amenable to coding for cladistically based tree approaches. Usually, one must arbitrarily break up the values of a continuous scale (such as body mass) into arbitrary divisions, to code them as character states (so body mass could be arbitrarily coded as small, medium, and large).

Fink and Zelditch (1995) suggested that the relative warp scores, which are effectively shaped components of a specimen relative to the reference configuration, could be used as characters to construct phylogenies and employed such scores to support the monophyly of the genus *Pygocentrus*. By using smaller specimens or outgroup specimens as reference configurations, they performed regressions of various partial warps on body size and used statistically significant differences between regression slopes as a means to define character states. The claim here is that the so-called partial warp scores would capture local differences in shape between specimens and therefore would be good at spotting changes in, for example, head, fin, or tail shape of fishes.

Although this may be a fruitful application of geometric morphometrics to phylogenies, there may be some hidden and quite significant sources of error. Remember, above, the description of how relative warps are calculated from a reference configuration, which is where the so-called shape space intersects the tangent space, from which all deviations, including relative warps, are calculated. As you change reference configurations, the angular relationships between specimens and the reference configuration changes in the shape and the tangent space, which changes the partial warp scores, often in unpredictable ways. Adams and Rosenberg (1998) analyzed a specific data set and found strong instability in phylogenetic groupings, depending on the choice of reference specimens and the resultant employment of different sets of partial warp scores. Rohlf (1998) argued that the partial warp scores cannot be said to have any biological meaning and also argued that changes in choice of reference configuration imparts unpredictable changes in the partial warp score. Of equal importance is the lack of statistical independence of the partial warps, which means that they cannot truly be considered as independent characters. Unfortunately, as Rohlf concluded, it may not be a trivial task to convert geometric morphometric parameters into characters that can be coded and used in the establishment of trees.

Because geometric morphometrics is likely to be the way most shapes are described in the next few years, we can only hope that it will be possible to adapt geometric morphometric data to phylogenetic approaches (see chapter 2). Agreed, the variables used to describe morphometric differences, partial warps, have no particular biological significance, except by coincidence. But, like all morphological characters, partial warps may very well provide data that define evolutionary innovations and shared derived characters, the very requirements of a phylogenetic approach to morphological analysis (Zelditch, Fink, Swiderski, and Lundrigan 1998). If partial warp scores tended to lead to wholly different conclusions with regard to homology, depending on the selection of slightly different reference forms, then we should view with skepticism the enterprise of phylogeny construction using these characters. But what if they work? What if there is not sufficient morphological difference among specimens that the instability is minimal and insensitive to minor differences in reference form selection? Zelditch et al. argued that the ultimate justification of any choice of morphological variables is their success in producing a set of homologous characters, and partial warp scores are no different in this respect from other characters. It remains for future studies to examine this issue with studies using total evidence and comparisons of data sets.

The Main Points

1. As a departure for studies of adaptation, a model must be devised that relates form, function, and evolution. The simplest case would involve a function that could predict, from a set of first principles, a unique form. If this form is found in a matching habitat, we might conclude that the form's appearance involved adaptation.
2. A general algorithm to study adaptation must include the following elements: learning the function of the structure, understanding the phylogenetic context of the "rise" of the structure, identifying character states that are ancestral to the taxon in question, and using these as boundary conditions for models of functional optimality.
3. Any algorithm inferring adaptation is limited by several problems and features of organisms. First, behavior and habitat selection bring an organism into a milieu most harmonious with its form. One cannot be sure that the form as currently observed evolved in the current habitat.
4. The prediction of form from "first principles" is hampered in several respects. First, historical limitations of organisms will preclude the appropriate engineer's solution. Second, there may be more than one optimal solution, or even a series of such solutions. Third, the evolution of form might involve a continuing shift in the optimum. As size increases, aquatic organisms may encounter new hydrodynamic regimes, and the optimum form may therefore change.
5. Constructional morphology is an integrated approach to the evolution and functional significance of form. It explains form as the net result of phylogenetic historical factors, functional influences, and the constraints imposed by the synthesis of biological materials.
6. Theoretical morphology is the field that devises (usually) algebraic rules for growth and development. If the mathematical algorithm used to simulate growth

matches biological development, then the range of forms generated can be compared with the range found in nature. With independent criteria for performance, theoretical morphology is a useful tool to assess the functional significance of those biological forms that have appeared in biological history.

7. Using phylogenetic history, a restricted optimality model can predict improvements in performance based on adaptive evolutionary change from an ancestor with a specific set of traits. Such predicted restricted optimal forms may be quite different, relative to forms evolving from other ancestral ground plans.
8. Some key innovations may have been crucial in the origin and radiation of major groups but the demonstration of such innovations is difficult.
9. Allometry is the study of changes of shape with increasing size. An exponential equation is typically used to describe the relationship between two linear dimensions.
10. Allometric relationships have been cited as evidence for developmental constraints. Although a few cellular and quantitative genetic models have been devised to account for a rigidity of allometric relationships, the presence of trends across the overall allometric trend suggests that a strong developmental constraint may be lacking and that the dictates of function may contribute to most well-known large-scale allometric trends.
11. The analysis of covariation of traits can be combined with cladistic analysis to map the stability of character combinations during the history of a taxon. Certain relationships may survive long periods of speciation and morphological change in the history of the taxon. Such analyses can be the basis for hypotheses explaining the long-lived relationships as the result of genetic correlations, epigenetic constraints, or functional interactions.

CHAPTER 6

Patterns of Morphological Change in Fossil Lineages

Though the waterfall
  In its flow ceased long ago
And its sound is stilled;
  Yet in name it ever flows,
  And in fame may thee yet be heard.

— Dainagon Kinto, ca. 1000 A.D.

The Taxic Approach to Measuring Evolutionary Rates

Darwin (1859) predicted at first writing of *The Origin* that the rate of evolutionary change would be irregular. In *Tempo and Mode in Evolution* (1944), Simpson asked (p. 3): "How fast, as a matter of fact, do animals evolve in nature?" He confirmed Darwin's prediction that the rate of evolution is highly uneven and also concluded that bursts of morphological change are highly correlated with periods of cladogenesis. My purpose in what follows is to evaluate the means by which we measure rates of evolution in the fossil record, and what this means in our interpretation of variation of evolutionary rate. It is the conflation of speciation and morphological evolution that confuses us about the role of speciation in evolution.

Neontologists might think that paleontologists would routinely estimate the rate of evolution directly as the rate of change of morphological features such as size or number of spines. But surprisingly, these kinds of data have been collected, even to this day, rather sparsely and were not reviewed in great depth in Simpson's seminal monograph. Bed-by-bed collection is best applied to sections with continuous deposition and preservation (Hunter 1998). The greater the interval, the more one expects to see significant morphological change, but the chance of missing sections increases as well. This restricts fine-scale measurement of temporal morphological change to a few parts of the record. Much more commonly, paleontologists have used *taxonomic longevity* as an estimate of evolutionary rate. The *taxic approach* dominates paleontological thinking, in no small measure because of large-scale computer databases of the geological ranges of taxa.

The taxic approach makes the simple prediction that evolutionary rate (change in a value of a character per unit of time) is inversely proportional to taxon longevity.

Charles Lyell set the pattern for this approach in his *Principles of Geology* (1830–1833), by documenting the rate of disappearance of extant taxa as one sampled strata of increasing age back into the Cenozoic Era. Using mollusk species, he assumed a regular loss and, when discovering an abrupt irregularity, concluded correctly that some of the early Cenozoic record must be missing in Great Britain (Rudwick 1972). Lyell dismissed fossil mammals as useless in resolving Cenozoic stratigraphic questions because their disappearances back into time were so rapid that extant taxa could be identified as fossils only in the younger Cenozoic strata. This very comparison among mammals and mollusks has been revived twice in the past century (Simpson 1944; Stanley 1973a), and both studies argued from geological ranges for a more rapid tempo of evolution in mammals. Simpson assumed that the rate of morphological evolution was inversely related to taxonomic longevity. If taxa were short lived, then morphological evolution was rapid and rapid changes of species-level rank were occurring within a phyletic lineage. If morphological evolution was slow, then such change was too sluggish to produce many changes of significant taxonomic rank; hence, taxonomic longevity would be considerable.

Taxa have been used to measure evolutionary rates indirectly. In single lineages, anagenetic changes are often extensive, in the absence of cladogenesis. Biostratigraphers have routinely rewarded a fossil taxon species status if it was slightly different from the fossils below or above. In some cases, just the presence of a form in a specific formation resulted in a species-level designation. This means that many so-called species are anagenic transformational series, with little or no cladogenesis. Thus, there is a confusion: When species names change along a geological section, it may mean that morphological characters have changed within a nonbranching lineage or that branching may have occurred as well.

The Stratigraphic Record: How Much Do We Have?

What can we – and can't we – see? Just how good is the fossil record? Fossils were the prime instruments used to date rocks until the advent of radiometric dating. Even today, the faunal zonations of groups such as ammonites and foraminifera can often give a more accurate relative date for local correlations than can radiometry. But we also know that preservation is uneven, periods of nondeposition and erosion exist, and embarrassing gaps ruin complete records of change, even in the more continuous deposits of the deep sea. Is the record of sufficient quality to estimate rates of evolution and to locate sites of speciation?

To document evolutionary change in the fossil record, we would require the following: (1) a complete and continuous sedimentary record of a high and constant rate of deposition so that fossils could be collected throughout long local geological sections; (2) a good sedimentary record throughout the paleogeographic range of the taxon; (3) abundant and well-preserved fossils distributed continuously throughout each of the local stratigraphic sections; (4) markers of absolute time, to calibrate evolutionary change to sedimentary rate; and (5) indicators of the paleoenvironment. If any one of these requirements has not been met, we cannot precisely estimate evolutionary rates and patterns. The virtually insoluble problem of discriminating evolutionary change from localized ecophenotypic responses is also a continual impediment to determining whether morphological change truly represents evolution. For example, Bretsky and Kauffman (1977) found a progressive size decrease in a Paleocene lucinid bivalve mollusk, *Myrtea uhleri,* preserved within a regressive sedimentary sequence. A shape change was correlated with the size change, but juveniles also had the same shape throughout the fossil sequence. Was the trend merely one of increased mortality, thus leading to elimination of adults, or an evolutionary trend toward more "juvenile" morphologies?

The completeness of the sedimentary record. No place on earth has a complete geological record of Phanerozoic time. Even if a habitat appropriate for a certain group of species were present for a long time at one geographic location, periods of nondeposition or erosion would reduce the completeness of the stratigraphic record. Even when rocks are present, deformation or metamorphosis may have destroyed all but the faintest remnants of fossils. In southern New England, in the United States, for example, early Paleozoic sedimentary rocks are common but strongly metamorphosed; fossils are rare. As a result of localized metamorphosis and nondeposition, time periods of the order of 10 million to 100 million years are typically nonfossiliferous in a given region. If evolution has any geographic component, then major losses of transitional forms are inevitable. This loss is compounded by uneven exploration and problems of fossilization. An indication of the potential gravity of the problem is the positive correlation between total rock volume and fossil taxon richness (Raup 1976b; but see Sepkoski, Bambach, Raup, and Valentine 1981). This positive correlation may mean that a major component of taxon richness is simply a matter of sampling bias.

Even when the stratigraphic record seems to be continuous over a given time span in a given region, parts of the fossil record are missing. Some gaps are readily identified, because strata may lay on tilted and older beds that have been uplifted and eroded. In marine deposits, such obvious nonconformities, however, usually indicate that the entire marine environment was not present in the area during the time period, owing to a marine regression, so nothing of the habitat and evolutionary record has been lost. More worrisome are those stratigraphic gaps that represent nondeposition or even erosion, despite a lack of obvious change in the environment. This is especially likely in those terrestrial environments where fossils are preserved in stream gravels and sands that were not the typical living habitat of the organisms (Figure 6.1). Preservation in terrestrial environments of this sort is bound to be incomplete, and different local stratigraphic sections are likely to have sediments representing different spans of time. It would be instructive to discuss the problem of correlation among local geologic sections in greater depth from a detailed geological perspective, but we have space for only some generalities. The reader is referred to Shaw (1964), who pioneered the problem of correlating a series of geological sections, each of which is stratigraphically incomplete but in different portions of the section.

Schindel (1982a) helps to define the information that would be useful to know to quantify gaps within a geological section:

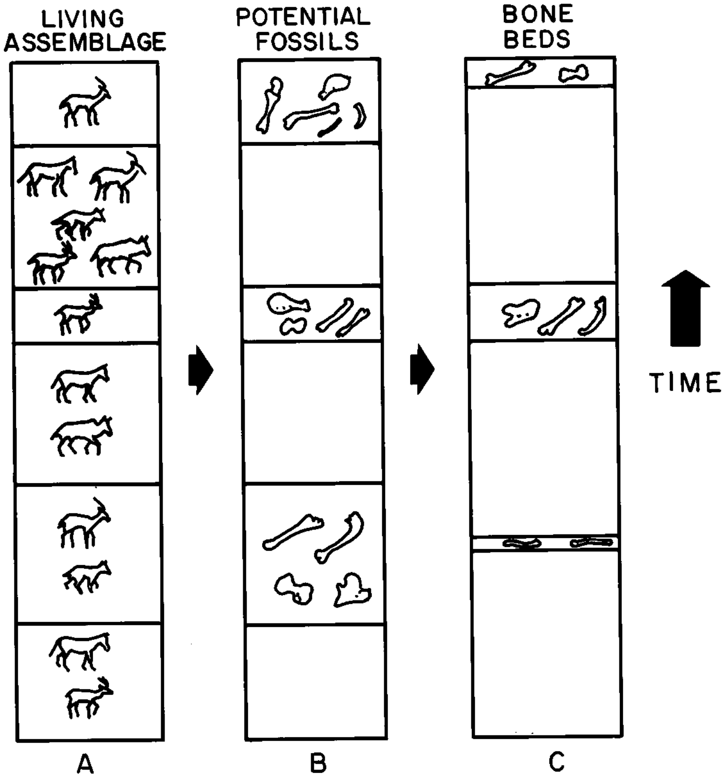


Figure 6.1. Schematic representation of loss of the representation of time intervals, as (**A**) living organisms die and are transported to (**B**) a site of deposition, and as these deposited fossils are either (**C**) buried or eroded.

1. *Temporal scope* is the total span of absolute geological time represented by the section. This information is essential for time correlations and for calculations of evolutionary rates.
2. *Microstratigraphic acuity* refers to the time represented by each fossiliferous stratigraphic sample (Schindel 1980). The degree of acuity is calculated from short-term rates of sedimentation, using modern environmental analogues. Large errors are likely.
3. *Temporal stratigraphic completeness* refers to the fraction of the temporal scope represented by strata, as opposed to time gaps. To make this measure meaningful, an absolute time period must be specified. Absolute time can be measured by radiometric dating, biostratigraphic correlations with radiometric markers, or magnetostratigraphic correlations. Thus, we can ask, for periods of *x* years, how complete is the record? If a resolution of 1 year is required, for example, the fossil record is usually woefully incomplete. But completeness for greater time spans can be useful for some kinds of evolutionary studies. Thus, for example, a stratigraphic section may be only 50% complete using a resolution of 1 year, whereas it is 100% complete at a 100-year resolution because there is at least 1 year present from any 100-year time interval.

In addition to these measures, we require others:

4. *Geographic stratigraphic completeness* is the proportion of the biogeographic range for any one time that is represented by sediments. Most evidence suggests the presence of strong geographic variation within species. There is also the possibility that a variant arising in a small area may then spread throughout the range of a species. Therefore, this measure can be crucial but has not been studied adequately.
5. *Sedimentation rate changes:* When recovering a core or studying a geological section, one rarely has dense absolute time markers, such as varves or bentonites. If the rate of character change increases rapidly within a small part of the section, two explanations are possible. Either the rate of phenotypic change did accelerate or the rate of sedimentation slowed markedly, giving the illusion of rapid change.

How complete is a sedimentary record? Sadler (1981) compiled over 25,000 published records of sediment accumulation and demonstrated that the time span (temporal scope) over which the sedimentation rate is measured explains much of the variance in rate. The estimated sedimentary rate is inversely related (Figure 6.2) to the temporal scope over which it is measured. This can mean only that long-term calculated rates have incorporated significant periods of nondeposition or erosion.

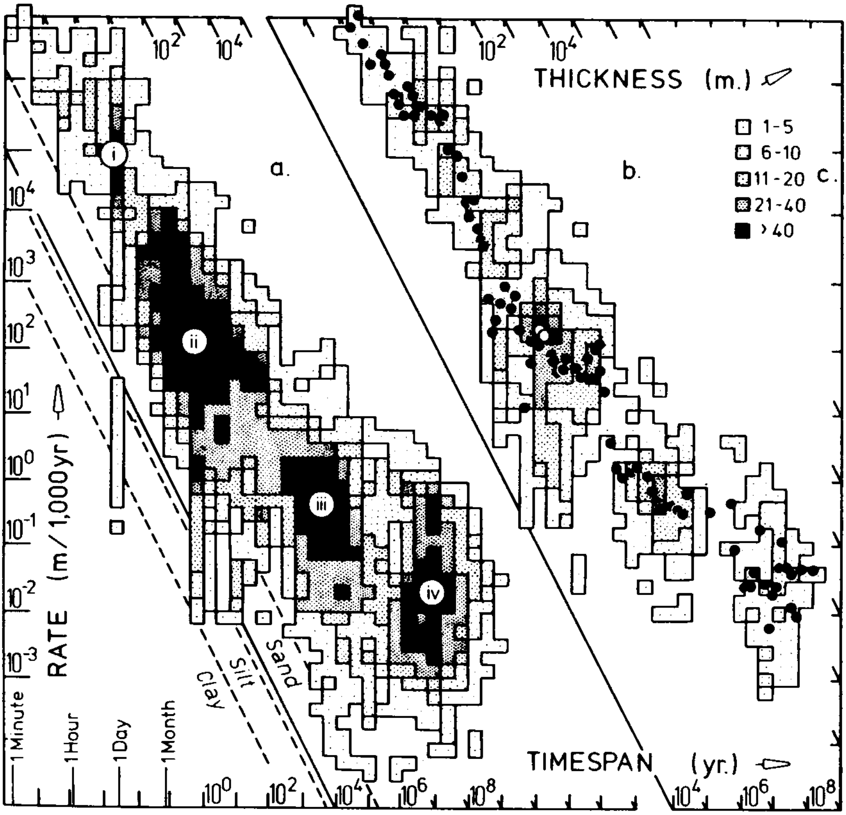


Figure 6.2. Relationship between estimated rates of sediment accumulation versus time scale over which rate was measured. (From Sadler 1981; reprinted from the *Journal of Geology,* 89:569–584, with permission from the University of Chicago Press.)

Calculated rates from thinner sedimentary columns are more likely to include particular portions representing continuous sedimentation. As the stratigraphic section to be measured decreases in thickness, the estimated sedimentation rate should converge on the true sedimentation rate for the appropriate environment (Sadler 1981). As longer time spans are usually represented by thicker sedimentary sections, sediment compaction would also cause an underestimate of the rate of sedimentation. This factor is a relatively minor component in explaining the overall variance of measured sedimentary rates (Schindel 1982a).

The inverse relationship between estimated sedimentary rate and temporal scope makes our chances of a complete sampling of evolutionary time increasingly remote when a finer time scale is required. For example, if we wanted a year-by-year record, the stratigraphic record used by Simpson (1944) to study the evolution of fossil horses is only 7% complete.

Temporal stratigraphic completeness can be estimated as the ratio of the accumulation rate, S, to the average rate of accumulation for a given smaller time scale, S^*. Alternatively, completeness can be estimated from the ratio of S to the average rates from a modern sedimentary environment similar to that represented by the rocks in question. Because of the overall negative relationship between estimated sedimentary rate and temporal scope, as the desired time resolution increases, the proportion of intervals at that time resolution represented by sediments will decrease. Temporal stratigraphic completeness, C, is

$$C = S/S_0$$

The gradient of rate to time span, m, is related to completeness. We estimate m from the empirical relationship between temporal scope and estimated sedimentation rate. Thus, $S = m\ln t$, where t is the temporal scope. If t_* is the time span of a given arbitrarily smaller time unit,

$$1\mathrm{n}S/S_* = m\ln t - \ln t_*$$

Thus, completeness is estimated by

$$C = S/S_* = (t_*/t)^{-m}$$

Sadler (1981) gives a useful example, based on the depositional rates of platform limestones, the source of much of the invertebrate Paleozoic record. Consider a 900-meter limestone section deposited over 15 million years. What is the completeness of the section for intervals of 5 million years? On the basis of available data, mm = -0.35 and $C = (5/15)^{.35} = 0.68$. In other words, one of every three 5-million-year intervals will not be represented by sediment. Is it any wonder that large gaps exist? Darwin was quite right in believing that at least some of the major gaps in the fossil record might be explained by lack of preservation. Most would agree that 5 million years is enough time for much to happen; for such a loss to occur a third of the time is to guarantee significant losses.

There is a minor fly in the ointment of the inverse rate story, because of the means of plotting time versus its inverse rate, more low rates will be found as the temporal scope increases if sediment deposited is more or less constant. Even random numbers can give a spurious correlation, which can reach 0.7. Schlager, Marshal, van der Geest, and Sprager (1998) avoided this problem by performing direct regressions of thickness and time, over a number of time classes for carbonate and siliciclastic rocks; estimated sedimentation rates still decreased systematically as the temporal scope increased. Thus, the inverse relationship of estimated sedimentation rate to temporal scope is not simply an effect of the mathematical transformation. Sedimentation is an episodic process, and the sediment record is riddled with hiatuses on all scales.

Many studies of the rate of morphological evolution involve relatively short time intervals of well-preserved sediments. Of eight such studies tabulated in Schindel (1982a), only two have temporal scopes over 12 million years and four are below 2 million years. In a study by Williamson (1981), the overall sedimentation rate estimated from the total section is much higher than expected from the average relationship of lacustrine sedimentation rate to temporal scope. This is probably due to the proximity of the sedimentation site to a tectonically active area. Williamson was thus able to document morphological changes over a period of only 0.4 million years. A study by Sheldon (1987) of an extraordinary Ordovician section in Wales estimated a stratigraphic acuity of only 900 years.

Figure 6.3 gives stratigraphic completeness for the eight studies. At the level of 10^5 years, most of the samplings are virtually complete, though two show large gaps. The famous bed-by-bed *Kosmoceras* study by Brinkmann (1929; Raup and Crick 1981, 1982) is less than 30% complete even at this coarse time scale. At the level of 10^4 years, most of the studies are less than 50% complete. That is to say, less

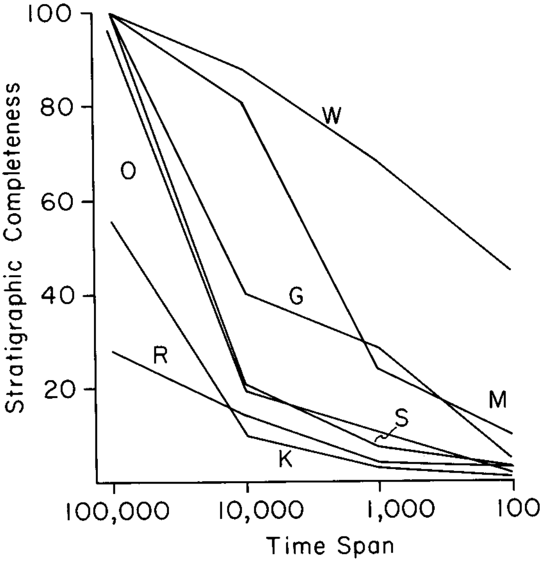


Figure 6.3. Relationship between stratigraphic completeness and time span represented by the deposit. (Data from Schindel 1982a. G = Gingerich 1976; K = Kellogg 1975; M = Malmgren and Kennett 1981; O = Ozawa 1975; R = Raup and Crick 1981; S = Schindel 1982b; W = Williamson 1981.)

than half of the expected intervals of 10^4 years, could be sampled. This is alarming, as much evolutionary change can happen in 10,000 years. It takes only modest selective pressures to shift many morphological features to a significant degree over such time scales, given the relatively short generation times of many invertebrate groups. These estimates are to be taken with caution, because (1) they assume that the total column has been compacted by a factor of two (Schindel 1982a) and (2) the short-term sedimentation rate used from more general data to calculate completeness may not be representative of the particular study.

These few analyses can lead to only provisional conclusions, but they also represent cases in which preservation was believed good enough to investigate rates of evolution. The cited examples thus are probably better than the typical situation for the fossil record as a whole. The generally poor representation of 10,000-year intervals is discouraging, as speciation probably acts on this time scale in many cases. The situation is, in reality, far worse, as we have not taken geographic stratigraphic completeness into account. The relative completeness seen between the 10,000- and 100,000-year levels of resolution suggest that only general trends may be observable with fossil data.

In some cases, major increases in evolutionary rates may be correlated with changes in sedimentation regime. Barrell (1917) first discussed the general pattern of shifting wave energy and sea level as related to potential cycles of sedimentation. He argued that a general base-level depth existed, above which erosion was common. During a lowering of sea level, this baseline would shift seaward, and records of evolutionary responses to shallowing would tend to be lost.

Speciation would be expected to occur, for the most part, in the shallow parts of marine basins, which are ecologically and geographically marginal (e.g., Eldredge 1971; Emiliani 1982; Jeletzky 1955). These are the very sites where geographic and temporal stratigraphic completeness are likely to be minimal. The more complete central basins may be sites of more continuous sedimentation, but they may not be indicative of the general tempo of evolution. It thus seems likely that speciation would not be commonly observable in the fossil record. This is amply confirmed by the many careful studies showing the apparent effects of cladogenesis but failing to show exact patterns of ancestry (e.g., Fisher, Rodda, and Dietrich 1964; Kaufmann 1933; Lang 1919).

What Is The Rate of Evolution in Fossil Lineages?

A measure of evolutionary rate and Haldane's paradox. Rates of morphological evolution were compiled, principally for vertebrates, long before the bias of stratigraphic completeness was discovered. We owe most of our knowledge of these rates to the pioneering work of George Gaylord Simpson, who compiled data principally for horses in *Tempo and Mode in Evolution* (1944). These rates were usually based on differences in sizes of various structures between taxa living at different times, with relatively poorly understood cladogenies below the level of the genus. The differences were usually accompanied by some unknown degree of cladogenesis as Simpson indicated. By the time of the writing of Simpson's classic, it had long been known that even modest selection pressures could shift morphological traits in populations by large degrees in only a few thousand generations. As early as 1915, Punnett had reported calculations showing that a favored genotype could rapidly increase in frequency in a population. It was thus of great interest to see how such changes occurred over the temporal scope of millions of years available to paleontologists.

Simpson's compilation and other data on fossil reptiles were used by Haldane (1949) to calculate proportional rates of change for linear measurements. Over a time, δt, a structure may increase in size from x_1 to x_2. The proportional rate of change is

$$\frac{\delta \ln x}{\delta t} = \frac{\ln x_2 - \ln x_1}{\delta t}$$

Of course, to proceed, we have to ignore Simpson's finding that there is no straight-line track from the smallest to the largest horses (which Haldane *did* ignore, but he was only a geneticist!). Between the fossil horse taxa *Hyracotherium* and *Mesohippus,* paracone height increases from 4.67 to 8.36 mm. The proportional rate of evolution is, therefore, 0.5823 divided by the time, 16×10^6 years, or 3.6% per million years. Haldane proposed a convenient measure, the darwin, which equals a change by a factor of *e* per million years. On a semilogarithmic scale (time versus natural logarithm of length), a rate of one darwin would correspond to a difference of one logarithmic unit per million years. For the above example, the rate is 1.036/2.718, or 0.38 darwins. The overall estimate of vertebrate evolutionary rates on the order of a few percent per million years has been generally reported since Haldane's estimates (e.g., Kurtén 1959a). Some much larger rates have been reported for invertebrates. Swinnerton's (1940) study of the Liassic *Ostrea–Gryphaea* lineage yielded a size change of 1% in about 3,000 years, whereas Teichert's (1949) study of a Permian crinoid yielded a rate of change in bulk of the basal plates of about 1% per 600 years.

Haldane also calculated the time, T_{SD}, for a trait to change by one standard deviation in size as

$$T_{SD} = Vt/(\ln x_2 - \ln x_1)$$

where V is the coefficient of variation. For the evolution of the paracone from *Hyracotherium* to *Mesohippus,* it would take half a million years, assuming a generation time of three years. Estimates for other mammals and foraminifera give results of similarly low magnitude (Charlesworth 1984a). This is remarkably slow, considering laboratory selection experiments that can accomplish the same degree of change in a few tens of generations (Mather and Harrison 1949; Robertson and Reeve 1952). Thus, *Haldane's paradox* was raised: Why is evolution in fossils so slow? Haldane argued that the data from the fossil record did not strongly support the action of natural selection in affecting phenotypic evolution. He suggested mutation pressure as a possible alternative hypothesis. This would be in strong contrast to Simpson's belief that natural selection had been behind the evolution of hypsodonty in horses. The calculation does not take into account the joint evolution of different characters, but it is not entirely clear that this would make a great deal of difference (Charlesworth 1984b).

Using a quantitative genetic model, Lande (1976) calculated the minimum selective mortality necessary to generate the commonly observed rates of evolution in the fossil record. He assumed that the character under selection follows a normal distribution and that fitness is a normal function of phenotypic value, which can be estimated along a linear scale (e.g., length). Truncation selection is used as the mechanism of directional change. Heritability cannot be calculated for traits belonging to fossil taxa, but a range of values known for analogous living forms might be useful in setting bounds within which drift might be excluded as a force in evolution. Lande assumed that a genotype–environment interaction is absent, and that heritability, h^2, and phenotypic variance both remain constant during the period of change. If z is the amount of phenotypic change, and σ the standard deviation, then a calculation of $z\sigma$ (see Lande 1976 for details) permits a further calculation of the proportion of the population culled each generation to cause a given rate of evolution from natural selection alone. The effective population size, N^*, at which there is a 5% chance that genetic drift can cause a change of z over t generations is

$$N^* = (3.84h^2\mathrm{t})/(z/\sigma)^2$$

If the effective population size is greater than N^*, then drift can be excluded as a likely hypothesis. There is a likely bias in the estimate of σ. If we are combining a time-averaged sample of fossils, where the mean value of the trait changed significantly over time, σ will be inflated.

Lande (1976) calculated for Tertiary mammals that the mortality necessary was only about 1 death per million per generation. Observed rates, moreover, are slow enough to have been caused by genetic drift occurring in effective population sizes of 10^4 to 10^5. If stabilizing selection was weak, horse evolution could have occurred by genetic drift between the browsing and grazing adaptive zones described by Simpson. With moderate stabilizing selection, however, directional selection would almost surely have been required to produce the trend.

Reyment (1982a) made a similar calculation for phenotypic evolution in a fossil ostracod lineage. In the Upper Cretaceous of Morocco, an anagenetic evolutionary event at the transspecific level, from *Oertliella tarfayensis* to *O. chouberti,* can be identified by a change in surface ornamentation and other characters, which exhibit a transitory polymorphism over 1–2 × 10^5 years. Length of carapace also changes, but Reyment's calculation shows that, assuming a heritability of 0.2, selection could have been accomplished with 1 selective death per 10^{11} individuals per generation. Drift could have occurred in populations as large as 2.7 × 10^6, which is far larger than thought to be likely for ostracod populations. Reyment questioned whether such a univariate expression of change is meaningful and suggested that stronger selection might have been required to change the entire morph from the ancestral to the descendant state. Reyment (1982a) inferred higher selective mortality, on the order of tens per hundred thousand per generation, in another study of megalospheric proloculus size in the Cretaceous foraminiferan, *Afrobolivina afra*. Depending on the heritability, N^* falls within the range of 10^4 to 10^5.

Charlesworth (1984b) estimated the genetic load associated with directional selection needed to account for observed rates of change, when the simultaneous load of stabilizing selection is taken into account. On the basis of published cases of vertebrate and foraminiferan evolution, the calculated cost of directional selection is usually astronomically small – on the order of 10^{-10} – and is still on the order of 10^{-6} if variation in direction of evolution is taken into account. He argued that these estimates are on the conservative side and that directional load is probably overestimated. If we consider multiple character evolution, genetic correlations among characters will reduce the load, relative to that calculated as the sum of independent directional selection on single characters. Charlesworth's calculated loads for single characters are so low as to make the evolution of several independent characters possible with little load.

These calculations make the paradox clear: The rate of evolution is so slow as to defy the conclusion that natural selection is the main driving force of morphological evolution.

The incomplete record and measures of evolutionary rate. Haldane's paradox can be viewed in the light of our discussion of the temporal completeness of the sedimentary record. An apparent inverse relationship exists between temporal scope and the measured rate of sedimentation. This can be explained by the presence of gaps in deposition, whose cumulative effect is an apparent slowing of sedimentary rate as more sedimentary column is accumulated and more gaps in sedimentation are added. By analogy, is it possible that Haldane's paradox can be explained by the addition of periods of rapid evolution and periods when virtually no evolutionary change or reversals occur? The slow rates of change, after all, are usually measured over periods of millions of years. Given the low stratigraphic completeness of most cases, it would be difficult to identify change over periods much shorter than 100,000 years. Indeed, many terrestrial bone beds in fluvial deposits can be shown to be agglomerations of about 1,000 to 10,000 years (Behrensmeyer 1982). The theoretical studies of Kirkpatrick (1982a) and Petry (1982) show that conservative values of selection intensities and genetic variation could easily result in large-scale changes within the cracks of the geological record. Could one ever see rapid rates of evolution in the fossil record?

A compilation of evolutionary rates uncovered a bias analogous to the sedimentary rate relationship discovered by Sadler and Schindel. Gingerich (1983) compiled rates of morphological evolution (Figure 6.4) for laboratory selection experiments (averaging 50,000 darwins), historical colonization events (about 400 darwins), faunal changes following Pleistocene glaciation (about 4 darwins), and lower rates from the vertebrate fossil record, such as those used by Haldane and Lande cited above. Overall, measured evolutionary rate is related inversely to the time scale over which the change was documented. This result suggests that much of the basis of our belief in the low rate of fossil evolutionary change is incorrect, especially

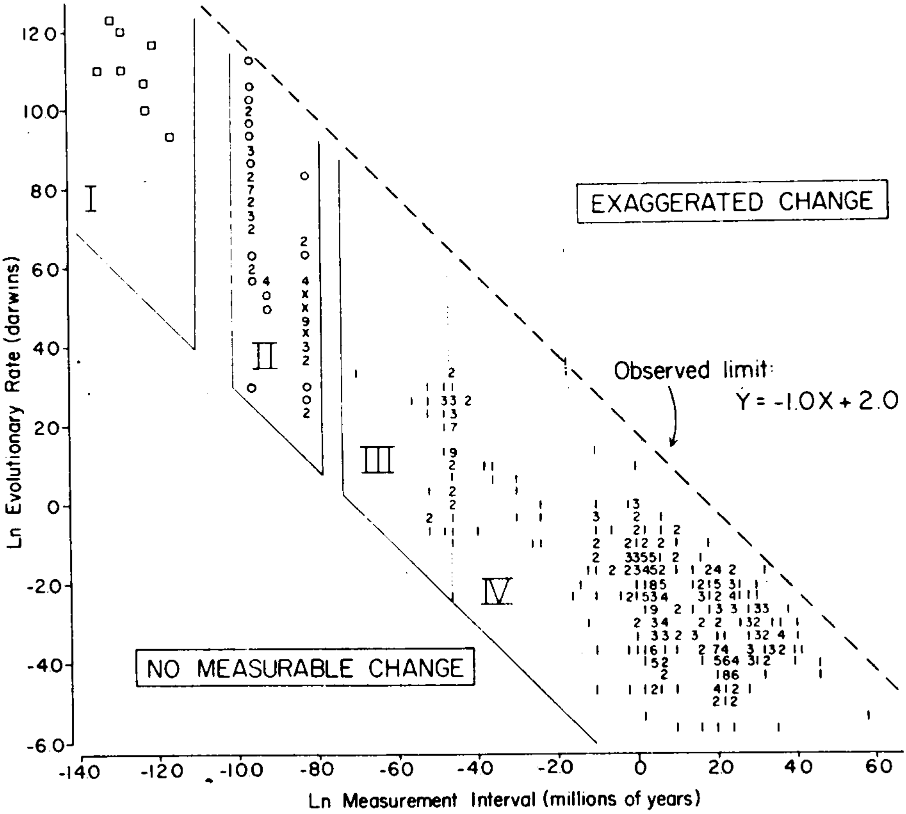


Figure 6.4. Inverse relationship between temporal scope and estimated rate of morphological evolution. Domains I to IV correspond to rates from laboratory selection experiments, historical colonization events, recovery from Pleistocene glaciation, and fossil invertebrates and vertebrates, respectively. (From Gingerich 1983, with permission.)

because the average ratio of the initial to the final states used to calculate the evolutionary rates is about 1.2. As Gingerich argued:

> Organisms differing by a factor of much more (or less) than 1.2 are so different (or so similar) that they are rarely compared in calculating rates, regardless of the time available for one to have changed into the other. The net effect of such a stable difference between initial and final morphological states over all time intervals studied is to make interval length the principal determinant of rates. The greater the time separating similar initial and final states, the slower the inferred rate of change.

The negative relationship between evolutionary rate and temporal scope might be an artifact, as there is an apparent homogeneity of proportional morphological difference, about 1.2, used in the calculations of evolutionary rate (Gould 1984a). If a difference of 1.2 is used over 1 year or 1 million years of time, then a negative relationship between time and rate is inevitable. If true, then one is effectively plotting k/t as a function of t, where k is a constant and is equal to 1.2. This complaint is similar to the one answered by Schlager et al. (1998) for sedimentary rates. This result, however, represents much more than a mere artifact of plotting. As Gingerich

(1984) noted, change is not constrained to 1.2 and varies substantially. Moreover, it is doubtful that workers looked only for those proportional differences of 20% and then divided by the time that coincidentally had been covered. Rather, this spectrum of rates gleaned from the literature represents a wide range of studies. There is no constraint that would set the average rates for laboratory populations to be so rapid. Artificial selection *is* potent and brings about changes of several standard deviations within a few tens of generations.

There is a more important mechanistic argument that suggests that Gingerich's result is more than artifactual. Short-term rates are probably biased toward those cases in which change has been observed; other cases in which change failed to occur are probably not reported, especially in laboratory populations and island invasions. Of course, the same is true for fossil lineages. One can therefore assume that the data are biased toward maximum change. If the estimate of rate is slower in fossil finds, one can argue that this is not for lack of a search for rapid rates. It is only the apparent mixture of rapid rates of change with periods in which no change occurs at all that produces relatively slow apparent rates of change in the long-term fossil studies (Gingerich 1983).

Much earlier, Kurtén (1959a) recognized much the same bias in the rates of morphological evolution in fossil mammals. Typical rates gleaned from Pleistocene examples were 20 to 25 times as fast as those taken from older deposits in the Tertiary. Although the rate of morphological evolution could be somewhat greater in the Pleistocene, owing to rapid environmental shifts, Kurtén concluded that time scale was the major determinant. He noted that the slower rates taken from the Tertiary may be "partially or wholly spurious" because "they are without exception based upon samples millions of years apart, and the intervening histories may have contained any amount of fluctuation at higher rates" (Kurtén 1959b, p. 213). Kurtén recognized that reversals would reduce the apparent maximum rate of change if the temporal scope was long enough.

One might argue that Gingerich's and Kurtén's results combine inappropriately a diverse assortment of evolutionary rates calculated from very disparate types of data. But a study by Tom Phillipi (see also Bell, Baumgartner, and Olson 1985) on a much finer scale produced a similar result for rates of morphological evolution measured over different temporal scopes in the Miocene stickleback *Gasterosteus doryssus* (T. Phillipi, 1986, unpublished). Here, a presumed temporal scope of about 100,000 years was inferred from lake varve dating. The same negative correlation between measured rate of morphological evolution and time period was found in four of six characters that were examined (Figure 6.5). Reversals in evolutionary direction are partially responsible for the overall negative relationship between temporal scope and estimated evolutionary rate.

High rates of change in one morphological direction in selection experiments cannot be expected to be maintained over more than a few tens of generations. Exhaustion of genetic variability (assuming population size to be quite small and selection quite strong), the pleiotropic effects of genes, or interlocus interactions will probably preclude rapid change beyond a given point. It is also unlikely that selection will be so intense and similar in direction over long periods. Otherwise, we would

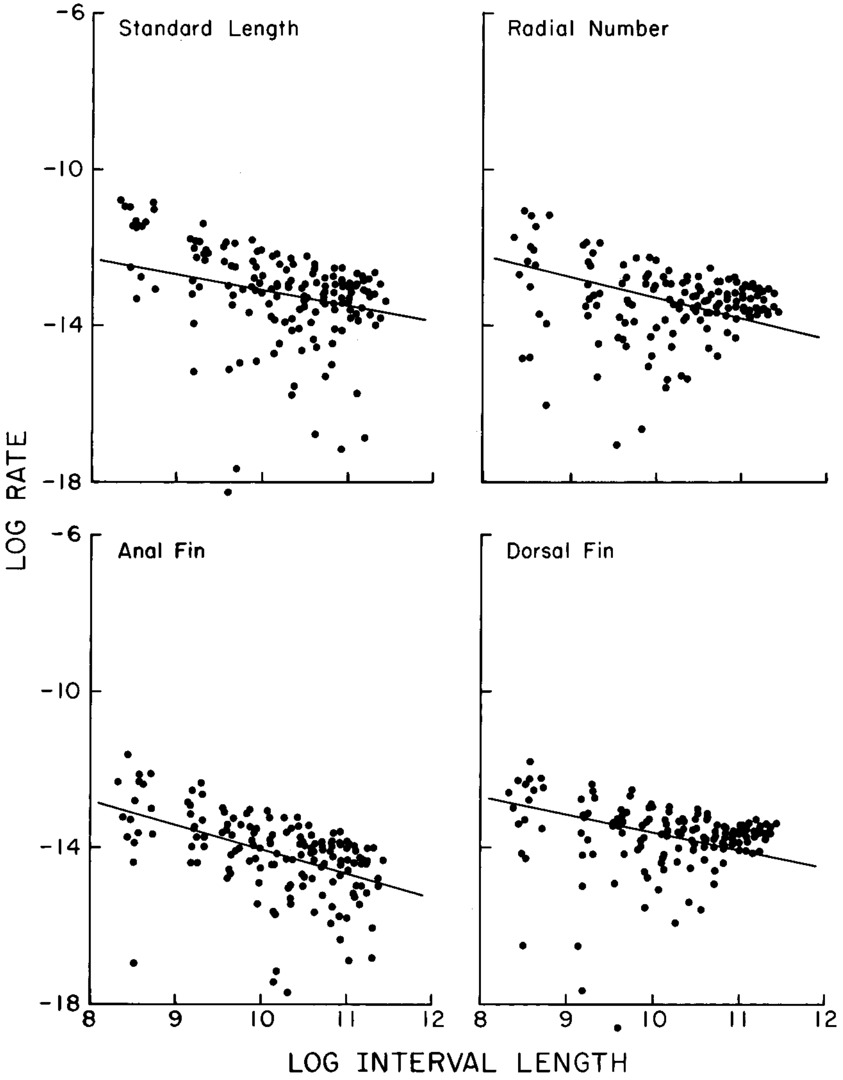


Figure 6.5. Evolutionary rate versus time interval in the Miocene stickleback *Gasterosteus doryssus*. All slopes are significantly negative, but no relationship was found for two other characters. (Courtesy of Tom Phillipi.)

eventually have mice as big as dump trucks and elephants the size of the moon, which is absurd. Variation in rates and direction of selection will appear as low rates of evolution when integrated over geologically long periods of time. The net rates measured for invasions, of the order of 400 darwins, may be typical of adaptive radiations and ecologically driven changes during speciation events. These would be difficult to identify, given the generally poor resolution seen in the fossil record. Differences between closely related mammal species are often of a magnitude of 0.1 to 0.2 *e*, a difference that could arise in an interval as short as 250 to 500 years, given rates of 400 days. The data of Bell et al. show that this effect will be registered at timescales usually at the finest level of resolution available to most paleontologists.

In the case of sedimentary columns, some minimal units of deposition can be used to determine the maximum rate of sedimentation for certain conditions. Can this be done for evolutionary rates? A plot of net evolutionary change, in terms of standardized normal deviates, as a function of time might yield three alternative outcomes (Figure 6.6). If net change is zero, then we have stasis, but a nonzero-slope straight line reflects a sustained directional change over time. A random shift can also occur, which will yield a range of changes. A plot of evolutionary rate as a function of time interval in generations makes this point more clearly. If the slope of such a relationship is zero, then the same rate is measured despite the timescale over

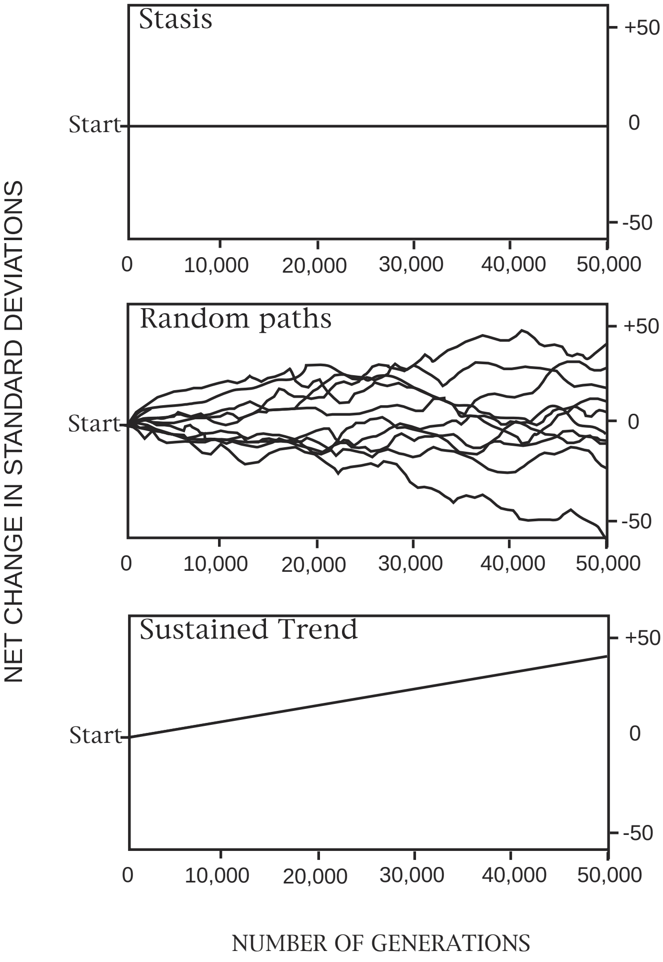


Figure 6.6. Plotting amount of evolutionary change with elapsed time (top) can yield three alternatives: (1) no change or stasis, (2) random change, (3) sustained directional change. Middle: Plot of rate of change as a function of elapsed time in *Hyracotherium grangeri,* which reflects stasis. Bottom: Plot of rate of change as a function of elapsed time in *Mus musculus,* which reflects a directional process. (Middle and bottom after Gingerich 1993b.)

which it is measured, which allows us to conclude that directional change is occurring. Alternatively, the slope of such a relationship might have a slope of –1, which indicates stasis. The majority of random walks are intermediate, as confirmed by simulations (Gingerich 1993a). Thus, under nearly all circumstances of change, there will be a negative relationship between evolutionary change and time interval; it is the slope that matters.

Gingerich (1993b) used this approach to examine change in Cenozoic horses and rodents (Figure 6.7) and extrapolated data at intermediate temporal scopes to one generation (making reasonable estimates of generation times) and found the remarkable result that evolutionary rates on the scale of one generation were in the range found for living populations undergoing strong directional change. In other words, when the proper scale is used, there is no evidence of slow rates of evolu-

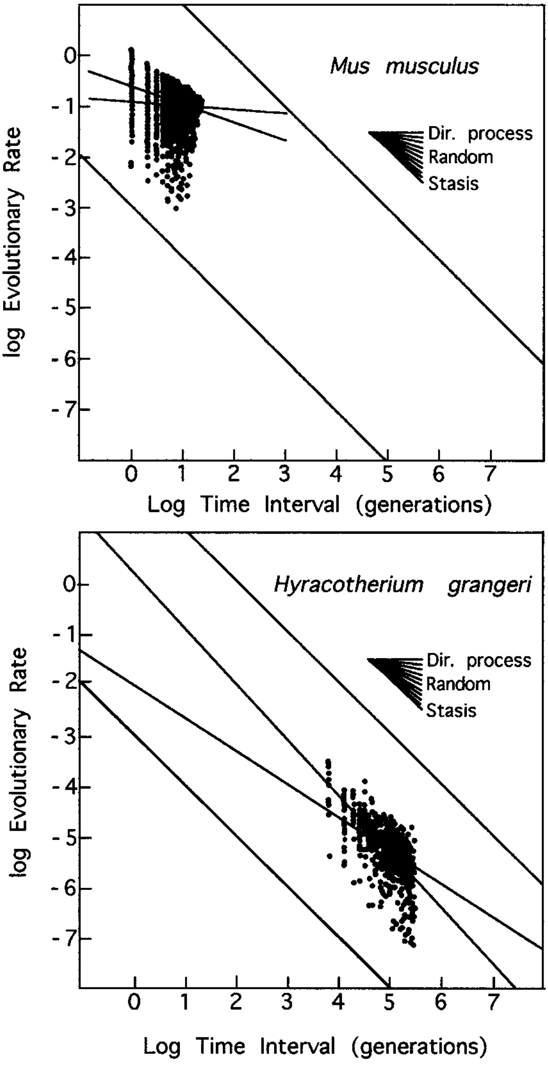


Figure 6.7. Two examples relating log rate versus log time interval. Top: Estimates of rates in *Mus musculus* are relatively insensitive to time interval, supporting a directed process of evolution. Bottom: Estimate for the fossil horse *Hyracotherium grangeri,* where the relationship supports random change. (Modified from Gingerich 1993a with permission from the *American Journal of Science.*)

tionary change in mammals. Slow change is rather a net effect of longer-term shifts and evolutionary reversals, which may or may not lead to a net change. Haldane's paradox is solved completely.

The fossil record *invites* measurements of slow rates of evolution; both the uneven nature of evolutionary change and the gaps of the sedimentary record tend to conceal rapid evolutionary events. Haldane introduced us to the broad swells of evolutionary change, not the more brief violent chops. It is crucial to remember that there is no qualitative difference in mechanism required to generate either rate of change. The fossil record does not falsify the notion that the evolutionary genetics of populations can be extrapolated to large-scale changes, although it would be premature to say that these data confirm a homogeneity of process among changes registered over all timescales.

Phenotypes, Genetic Variation, and Phenotypic Evolution

Polygenic determination of traits. When considering change in phenotypic traits in fossil lineages, it is useful to understand the polygenic nature of most variation, including polymorphisms involving discrete morphological states. Believers in the possibility of macroevolution via hopeful monsters usually invoke mutants of major phenotypic significance (Goldschmidt 1940; Gould 1980a). This often is accompanied by the hope that so-called regulatory mutants will facilitate a switch between morphological modes. Under this argument, the dichotomy between major and minor genetic changes would be associated with regulatory and structural gene variation, respectively. As shown in chapter 4, developmental variation fits squarely within a neo-Darwinian framework, but paleontological investigations still depend on an understanding of phenotypic variation and its potential meanings.

Workers have often mistaken discrete phenotypes for discrete genotypes, explained by a single locus of large effect. Goldschmidt (e.g., 1945a,b) mistook the mimicry polymorphism in swallowtail butterflies to be under the control of a major switch gene. It is ironic that although Goldschmidt believed that intrapopulation variation was not the stuff of interspecific evolution, he used a classic example of *intra*specific variation to bolster his argument. Punnett, whose famous square has been used by many generations of students to diagram genetic crosses, first argued (1915) that mimetic morphs in the swallowtail genus, *Papilio,* could be explained by a single gene. His experimental evidence was impressive indeed. Crosses between mimetic and nonmimetic forms of *Papilio polytes* yielded segregating progeny of mimetic and nonmimetic morphs as if they corresponded to individual alleles at a single locus. Not only had a mutation apparently vaulted an otherwise unbridgeable chasm to a new adaptive mode but it had even seemingly targeted itself to an extant model species! This result squared well with the intuition that intermediate forms in evolution were maladaptive (half an eye, and so on), so single mutational leaps were a necessity.

But a major discontinuity found in an experimental manipulation need not imply an evolutionary leap. Mimicry in species of *Papilio* is under polygenic control, often with several tightly linked loci controlling color, wing shape, and pattern (Clarke and Shepard 1963; Turner 1977). Modifiers contribute to determining the phenotype. Crosses between strains of mimetic and nonmimetic races of *Papilio dardanus* often result in inferior mimics, for lack of the appropriate modifiers (Clarke and Shepard 1962).

Not all mutations comprising the mimetic phenotype of butterflies are small in effect. Some of the changes are quite large, particularly the effects on color differences. It is rare for a set of genes affecting a trait to all have equally infinitesimal effects. A polygenic basis is usually found in resistance to insecticides, for example, but genes with major effects are also known (Crow 1957). The compendium of Lindsley and Grell (1968) commonly shows alleles at a locus with a wide range of expression. Most evolutionary geneticists work on the assumption of a range of effects, despite the arguments of Fisher that all changes were underlain by mutants of small effects (Turner 1983b). Nothing in population genetic theory, however, prohibits hopeful monsters, in the sense of major new phenotypes explained by a single allelic difference. Rather, we expect that nearly all such mutants, even if bearing some useful characters, have egregious correlated traits that make them unlikely to take in the population.

The evidence so far accumulated shows, however, that most morphological traits examined are under polygenic control. We need not detail here the widespread evidence. Nearly every morphological trait in plants and animals ever discovered to have a genetic basis is under polygenic control (see Falconer 1981; Stebbins 1950; Wright 1978, chapters 6, 8). Color polymorphisms often segregate as one locus, but multilocus control is far more common. The effect of a typical polygene is on the order of 0.1 to 0.5 of the additive genetic standard deviation (Falconer 1981).

Polygenic control is not restricted to continuous traits such as bill length in birds (e.g., Boag and Grant 1981). Discontinuous traits such as digit number and vertebral number are under similar control, albeit in combination with thresholds that help determine the discrete phenotype (Green 1962; Lande 1978; Wright 1934a, 1934b, 1935a, 1935b). It is, therefore, incorrect to believe that mutational jumps must of necessity occur in the evolution of discrete phenotypes. The confusion goes back to the debate toward the beginning of the twentieth century over the relative importance of biometrical (continuous) versus Mendelian (discrete) variation (Provine 1971). This is a false distinction, yet the large mutation–small mutation false dichotomy lives on to haunt us.

The polygenic control of discrete traits can be confirmed to a degree by F1 and F2 crosses between strains that are monomorphic for two alternative discrete states. This was done by Wright for inbred strains of guinea pigs with different numbers of digits and by Green (1962) in crosses of inbred strains of mice with different numbers of presacral vertebrae. Consider one strain selected to produce a given number of complete digits. We would expect a series of genes to have a distribution of effects, with a maximum of effects centered between thresholds determining the discrete number of digits. A cross between two such strains (Figure 4.22) would yield an F1 progeny set with a distribution of genetic factors intermediate in genetic composition, but it may fall to one side of the threshold. Therefore, all progeny may have the same number of digits. Crosses in the F2, however, should show an expansion of the distribution of genetic factors, resulting in significant numbers of individuals straddling the threshold. In guinea pigs, this results in a large number of individuals with incomplete digits (Figure 4.22). It was the discovery of such modifiers that led Castle to agree that gradualism had an important role in evolution. Similar polygenic control was found for presacral vertebrae in mice (Green 1962). Expression in crosses among four inbred strains resulted in only seven qualitatively different presacral morphs, suggesting the presence of thresholds.

Thus, the genetic architecture of both discrete and continuous traits are both polygenic, and the genetic determination of the phenotype is a complex result of interactions among genes that perform different functions. The evidence suggests that control comes from much of the genome and usually cannot be restricted to switch genes of major effect. The polygenic determination of discrete traits suggests a confusion in the literature over *macromutations* and *hopeful monsters,* the terms suggested by Goldschmidt (1940) for mutations of major phenotypic effects, involving coordinated developmental changes in many characters. Discrete jumps in morphological variation should not be construed to be evidence for leaps explained solely by a single gene, though the latter certainly can occur. The negative pleiotropic effects of such mutants make their importance in evolution unlikely.

This argument, however, does not exclude discrete *morphological* variants whose prospective functional significance may be profound. Frazzetta (1970) found a new potential site for a jaw articulation in the maxillary bone of a bolyerine snake. This change, although of great potential functional significance, is rather easy to explain, given that joints often are controlled by effects resembling the threshold effects for vertebral articulations and toe number. A polygenically controlled thinning of the jaw at the point of the prospective joint, in combination with the crossing of a threshold for a developmental "instruction" to generate a joint, would be sufficient to result in the evolution of the new discrete character.

Canalization. Many traits have strongly reduced population variability. This can be a surprise, particularly in meristic traits, such as bristle number in *Drosophila,* where variability in populations might normally be expected. Waddington (1956) showed that many phenotypes are controlled by large numbers of genes but are nevertheless buffered against change caused by variation in the developmental environment. He termed this buffering *canalization.* The necessity for phenotypic invariance may be attributed to potential negative effects of phenotypic deviants on fitness. In *Drosophila melanogaster,* scutellar bristle number is canalized at a count of four (Rendel 1959). Strong selection can shift gene frequencies out of a zone of canalization and thus increase the potential for expression of phenotypic variability.

Canalization may be a common explanation for phenotypes that are widespread in a species with little variation, despite the underlying polygenic nature of the trait. With a mechanism to reduce phenotypic variance, selection has no variation on which to act, and temporal or geographic invariance in a trait may not be surprising. *Environmental canalization* occurs when the phenotype remains the same despite considerable environmental variation. It is of obvious adaptive value to be able to elaborate a single head, despite variations in environmental temperature. Other traits, such as surface epidermal melanin, hair density, and hemoglobin concentration in the blood are often not environmentally canalized and are instead phenotypically plastic. A more interesting form of canalization is *genetic canalization,* where the same phenotype occurs despite a range of genotypes (Wagner and Booth 1997). This is the type mentioned above in digit determination. Here, genetic mechanisms, namely modifiers, impose a genetic threshold, which stabilizes the phenotype. Such stabilization might be important enough to be maintained for many generations, even across species boundaries.

Phenotypic plasticity and alternative phenotypes. One must be careful to distinguish between the genetic architecture of phenotypic variability involving a multiallelic system and a single genetic program that allows a single genotype to respond to different environments by producing different phenotypes. Such *phenotypic plasticity* allows an individual to increase fitness within its lifetime, thus reducing the evolutionary cost of having an inappropriate phenotype when exposed to a given microenvironment. Phenotypic plasticity is a measure of the evolved phenotypic response to the environment (Via and Lande 1985). Proper expression of plasticity depends on the evolution of an appropriate genotype–environment interaction. Strong correlations between phenotypic expression of genotypes in the two environments will slow the evolution of appropriate alternative expression of different states of a phenotypic trait (Via and Lande 1985; Via et al. 1995). With perfect plasticity, all individuals can change their phenotype appropriately. This would not be so in the case of genetically determined polymorphism. Unlike environmentally induced polymorphism, a genetically determined polymorphism requires for its maintenance that the morphs compete within patches for resources (Lively 1986). This also obtains for partial genetic control of alternative phenotypes. Otherwise, a more generalized phenotypically plastic phenotype may be favored. These alternative strategies are evolutionarily stable. With complete plasticity, one might expect long-term stasis in a fossil population with jigs and jags about a mean phenotype or group of phenotypes. With genetic polymorphism, generated by niche subdivision, the opportunity for genetic divergence might be present. Sheldon (1996) took just such a *"plus ça change"* model to predict that phenotypic gradual evolution should be more common in diverse, biologically stable habitats where coevolutionary processes are more common and thus promote transient polymorphisms.

Phenotypic plasticity acquires a distinct importance for organisms that cannot disperse or have dispersal distances that are small, relative to the environmental grain. The barnacle *Chthamalus anisopoma* has two distinct morphs (Figure 6.8), one of which has a recurved test. The predatory gastropod *Acanthina angelica* induces this morph, which reduces the barnacle's vulnerability to attack. Barnacle populations exposed to predation are wholly dominated by the recurved morph (Lively 1986). Similarly, the marine bryozoan *Membranipora membranacea* makes spines on the periphery of the colony when approached by the predatory nudibranch *Doridella steinbergae* (Harvell 1984). Both barnacle and bryozoan are sessile, which makes movement to avoid the predator impossible. There is, however, a cost in both cases. The barnacle is not able to protrude feeding structures in an effi-

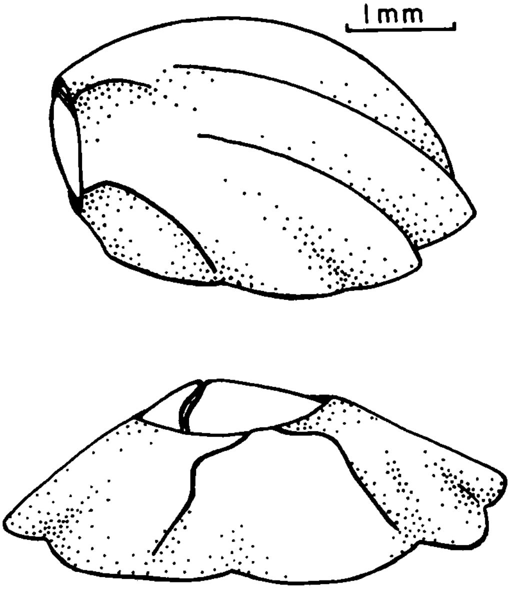
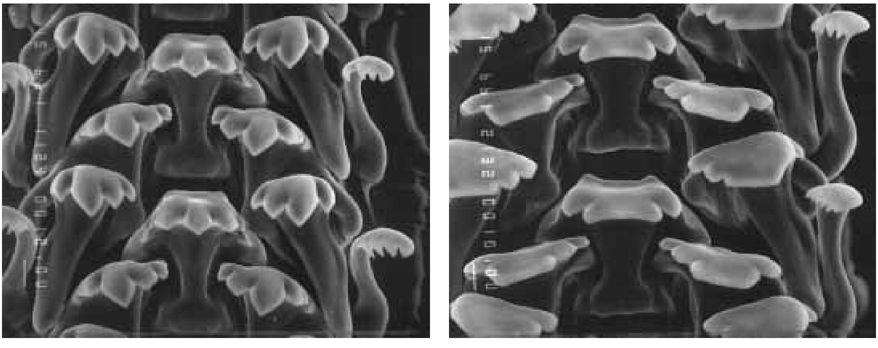


Figure 6.8. Two alternative morphs of *Chthamalus anisopoma,* an abundant acorn barnacle on Gulf of California shores. In the presence of drilling snails, the recurved morph helps deter attacks by snails. (Courtesy of Curtis Lively.)

cient manner, which makes the normal upright morph the "default," in the absence of predation. The bryozoan makes spines, but at the expense of the highest possible rate of colony calcification rate (Harvell 1984, 1992). Two possible radular morphs may be produced by the herbivorous gastropod *Lacuna variegata* in response to the presence of tough seaweed food or microalgae that must be shoveled from surfaces (Figure 6.9). Because radular tooth belts are discarded continuously, it is possible to switch from one phenotype to the other when the snail encounters a new food source. The turnover time is 17 to 40 days for *L. variegata* and 15 to 35 days for *L. vincta* (Padilla, Dittman, Franz, and Sladek 1996). Imagine this paleontological nightmare: two species (bryozoa, barnacles, gastropods) quite similar in morphol-



(a) (b)

Figure 6.9. Two alternative radular morphs of the snail *Lacuna variegata:* **(A)** The pointy teeth are produced when the snail is eating brown seaweed, whereas **(B)** the flattened teeth are produced when the snail scrapes microalgae from the surface. (Photos by Dianna Padilla.)

ogy with distinctly different morphology (spines, test shape, radular teeth) that are due only to phenotypic plasticity!

Phenotypic plasticity is not independent of genetic variation for the variable traits. Although a trait may be inducible, it is entirely plausible that some genotypes in the population are constitutive mutants that always express a single trait. Thus, in *Membranipora membranacea* described above, there are genotypes where the spined form is always expressed (Harvell 1998). Presumably, natural selection adjusts continually the balance between phenotypic plasticity and genetic polymorphism. If predation were a continuous feature of the environment, we would expect constitutive expression of spine formation to increase in the population.

Summing it up: The range of explanations of phenotypes. There are two alternative possibilities of genetically based phenotypic variation among individuals of a panmictic population, which we have discussed above (Figure 6.10). Genetic polymorphism would generate an array of phenotypes that might be able to sort to a set of appropriate microhabitats. But if inappropriate genotypes often find their way to a given microhabitat, then there would be a cost to population fitness. The alternative possibility is complete canalization, such that the phenotype is identical, regardless of possession of a range of genotypes and regardless of exposure to a variety of environments. Of course, genetic polymorphism can be said to blend into canalization. Dominance is a reflection of common phenotypic expression of more than one genotype. It has long been suggested that dominance is an evolved trait, securing the predominance of a phenotype that increases fitness. Finally, variation may be completely due to genes that effect a plastic response.

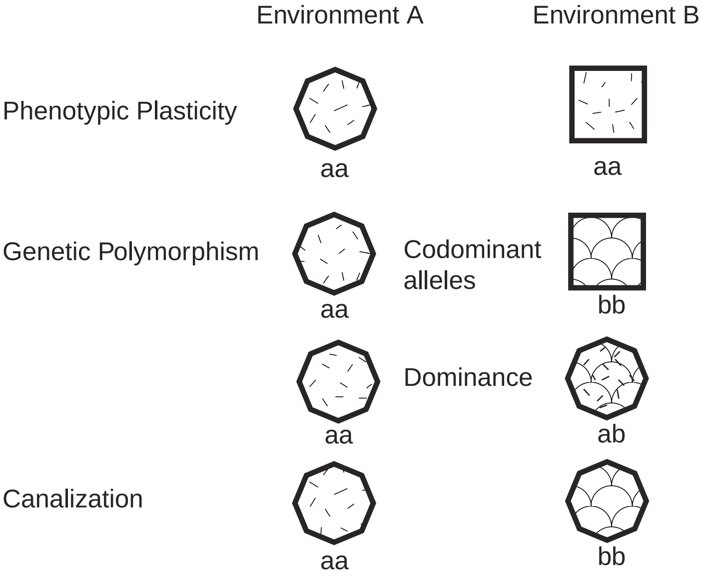


Figure 6.10. Relationship between genotype (fill pattern) and phenotype (shape of polygon) in the case of phenotypic plasticity, genotypic variation, and canalization.

Variation of the Rate of Evolution

Selection models and evolutionary rates. Proponents of the punctuated equilibrium theory (Eldredge and Gould 1972; Stanley 1979) have characterized neo-Darwinian selection models as predicting rates of phenotypic evolution to be slow and constant. A few points will clarify this major misconception. Indeed, the only model that predicts such slow and constant change is the neutral theory of molecular evolution.

Phenotypic shifts, when they occur, are liable to be rapid and of short duration, relative to longer-term periods of stabilizing selection. Mimicry, for example, should involve stabilizing selection as long as the model-mimic system remains intact. If a new model is introduced and becomes much more frequent than the previous one, a bout of intense directional selection will cause a rapid shift, assuming that available genetic variation permits the natural selective shift. Climatic shifts are often equally sudden and will select for rapid evolutionary change. The rapid phenotypic shift in Darwin's finches *Geospiza fortis* and *G. scandens,* in response to El Niño, is a good example (Grant and Grant 1989, 1993). Directional selection for a decrease of beak size followed an increase in predominance of smaller seeds. Such matching appears to be common for Galápagos finches, making the vegetation changes the important patterning for evolutionary rates and directions. Competition for resources also figures heavily in determining phenotypes of different coexisting species (Schluter, Price, and Grant 1985). Oddly enough, proponents of punctuated equilibrium (Jackson and Cheetham 1999) cite sudden environmental shifts as the basis for adaptation and subsequent stasis yet fail to see how this confirms the neo-Darwinian underpinnings of evolution. Speciation, when it occurs, is more the effect of natural selection than the generator of variation.

Both mechanisms of genetic determination of character state and some selection models suggest that rectangular (constancy, sudden change, then constancy) morphological evolution is to be expected, usually. When traits are discrete but determined by threshold effects, change may appear sudden but may be underlain by a large number of genes with an elaborate aggregate control over the discrete states of the phenotype. Thus, sudden changes of traits such as presence or absence of new ossification patterns (Alberch 1983) or the appearance of new ornamentation (Reyment 1982a) may be the result of rather simple genetic mechanisms (Levinton 1983).

Several models predict rectangular evolution of traits under directional selection with standard population genetic parameters (e.g., Kirkpatrick 1982; Petry 1982). If a trait is under polygenic control, and if there is environmental/developmental variance to the trait, sudden phenotypic shifts are to be expected if an environmental change involves (1) an increase in the relative height of an adaptive peak, (2) a decrease in the depth of a valley between two fitness peaks, or (3) a shift in position of two adaptive peaks, bringing them close together. A shift may also occur when an increase in overall mutational input to the phenotypic variance occurs or an increase in environmental–developmental variance in the character occurs. Either of these two changes may cause a chance movement of phenotypes toward another adaptive peak. A sudden shift in the location of a single peak could also cause rectangular evolution. This overall selection scheme seems plausible and would invariably predict rectangular evolution.

Let us look at one simple example of the Wrightian adaptive landscape to demonstrate how neo-Darwinian theory is consistent with rectangular phyletic evolution. Consider that instance in which a landscape has two adaptive peaks. If the mean population phenotype is located at one peak, nearly all random deviations will be insufficient to move it to an adjacent valley. But a rare random shift of this magnitude would result in an extremely rapid move (Figure 3.16), either back to the original adaptive peak or toward the second peak (Newman, Cohen, and Kipnis 1985). Indeed, gradual change would occur only if the landscape itself changes and if peaks shift gradually and unidirectionally. When the two peaks are static, and when the mean phenotype is near one peak, the expected time until a random shift between phenotypic adaptive peaks increases approximately exponentially with effective population size. By contrast, the expected duration of transition between the peaks is insensitive to effective population size, and the transition time between peaks is likely to be much too short to be detected by the level of resolution available in the geological record (Lande 1985). This would be true for either phyletic evolution or rapid phyletic evolution following or coinciding with a speciation event.

Thus, there is no reason to believe that alternating periods of stasis and sudden change represent anything more than the standard expectations of typical selection models. There is nothing compelling about this pattern that points toward the punctuated equilibrium hypothesis that speciation is the driving force of morphological evolution. Douglas Futuyma (personal communication, 1984) pointed out to me a possible exception to this conclusion. Suppose that adaptation to each of two ecologically distinct environments entails a complex of genetically independent traits. Reproductive isolation can prevent recombination between them, so that populations can diverge further in gene frequency and phenotypic space. Thus, speciation can act to stabilize multilocus genotypes and permit more extensive divergence.

The fossil perspective. What is the rate of evolution? The answer will elicit no real surprise: It is highly variable. This was one of the major conclusions first drawn by Simpson (1944), which derived from evidence for strong differences in taxonomic longevity, not from direct estimates of phenotypic change in geological columns. Brinkmann's (1929) classic study of the ammonite *Kosmoceras* suggested that apparent accelerations in phenotypic evolution might be correlated with diastems (small breaks in deposition) and that the actual rate of phenotypic change might therefore be constant. Teichert's (1949) study of the phenotypic evolution of the western Australian and Timorese Permian crinoid *Calceolispongia* revealed strong variation in rates of change in size and ornamentation. Figure 6.11 shows some of his evidence, which assumes constancy of sedimentary rate to relate stratigraphic position to time. The accelerated rate of evolution observed corresponds to Simpson's notion of quantum evolution, which implies occasional strong bouts of directional evolution.

In recent years, some have rightfully questioned whether patterns, usually reported only qualitatively, demonstrated either significant directional evolution or, if no net directionality was observed, significant variation in the direction of evolution (e.g., Gould 1976; Schopf et al. 1975). Raup and Crick (1981) used a runs test to demon-

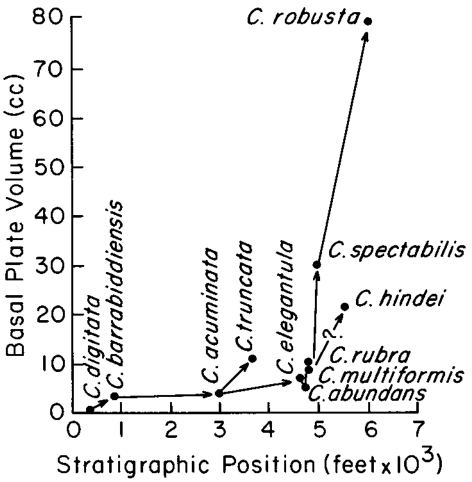


Figure 6.11. Increase of size of the principal "species" of *Calceolispongia,* as a function of stratigraphic position. (After Teichert 1949.)

strate that evolution in *Kosmoceras* was significantly directional but suggested that much random variation in rate might have occurred as well. (It should be mentioned, however, that the runs test has rather low statistical power.)

Bookstein, Gingerich, and Kluge (1978) used hierarchical linear modeling to examine variation in evolutionary rates and estimated the component of phenotypic evolution corresponding to linear change with elapsed time. In the Eocene *Hyopsodus,* studied by Gingerich (e.g., 1976), some part of the change was linear, but there was also a significant component of deviation from this temporal linearity. This is to be expected in any typical evolutionary case history. Charlesworth (1984a) looked at six cases of invertebrate and vertebrate studies of fossils using modified regression tests and found significant variation in rates in five cases. In a study of tooth dimensions (lower M2) in brown bears (*Ursus etruscus* → *U. arctos,* Kurtén 1959a), tooth size first increased steadily for 0.6 million years and then decreased for another 0.2 million years, with little net change over the entire period. In the Pacific foraminiferan *Globorotalia tumida* lineage (Malmgren, Berggren, and Lohman 1983), a sharp acceleration in the rate of size and shape change occurred at the Miocene–Pliocene boundary (Figure 6.12). Variation between levels, however, gives no indication that the transspecific change was anything but a transformation based on within-species variation (i.e., phyletic evolution). Tom Phillipi's (unpublished, 1986) analysis of the fossil stickleback *Gasterosteus doryssus* shows alternating periods of evolutionary change and stasis. Overall, there was no net change over the interval examined.

One might imagine a series of episodes of directional selection, with no net trend. After all, an environment might be constant over the long haul, but brief changes might cause deviations of environmental conditions away from the longer-term constancy. A study of 19 bivalve "species" lineages showed little change from the Pliocene to the Recent. The magnitude of change was usually within that found for geographic variation (Stanley and Yang 1987). This result is consistent with the notion of long-term stasis but not necessarily with the speciation requisite of the punctuated equilibrium theory. Bursts of phyletic evolution could be followed by approximate stasis for millions of years. Further, Cenozoic bivalve lineages consist

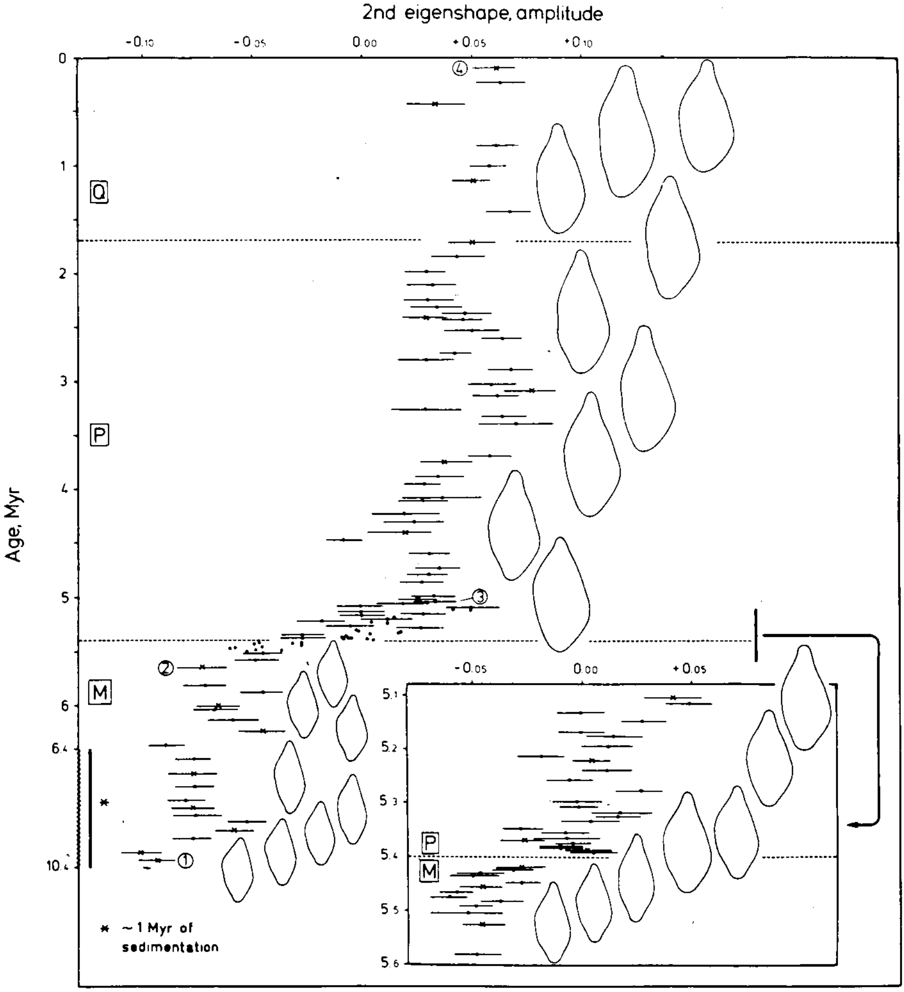


Figure 6.12. Variation in shape in the *Globorotalia plesiotumida* lineage, from the Upper Miocene to the Quaternary. Inset is a closeup of changes across the Miocene–Pliocene boundary. (From Malmgren et al. 1983, with permission.)

commonly of anagenetic strings of transitional species with little or no cladogenesis (e.g., Kelley 1983a, 1983b; Miyazaki and Mickevitch 1982). Stabilizing selection and canalization would be the explanation for stasis (Charlesworth, Lande, and Slatkin 1982; Stanley 1979, p. 57). Charlesworth (1984a) noted that even in cases in which no net change occurs in the mean of a phenotypic trait, significant variation in rate with fluctuating direction is the rule.

Can we measure the rate of evolution with fossil data? We would probably be able to make a convincing case at brief time intervals; as temporal scope decreases, the apparent rate should converge on the true rate. But it usually doesn't, at least as inferred from data such as in Figure 6.6. This raises the disturbing question of whether fossil data can be distinguished from a random walk (Bookstein 1987; Raup and Crick 1981). In the context of random motion, stasis can be defined as a statistically lower deviation from a starting condition than expected by chance. A directional rate of evolution should not be inferred unless there is a deviation from the starting condition that could not be explained by a random walk. Unfortunately, random walks look decidedly nonrandom to the eye. Coin tossing is often dominated by long runs of heads or long runs of tails. It is rare to see the end point of a long random walk process converge to the starting point, and individual runs often deviate in one general direction. To make things worse, estimated "rates" of change will decrease with increasing time intervals. In other words, the inverse relationship found by Gingerich (1983) could be merely a property of a random walk. An analysis of the foram data of Malmgren et al. (1983) suggests that there may be three phases of random walks at different overall rates, and not alternating phases of directional evolution and stasis (Bookstein 1987).

This argues for a healthy degree of skepticism over our current ability to quantify evolutionary rates and their meaning in the fossil record. It certainly seems premature to feel confident over whether rates can be used to distinguish genetic drift from selection. We have net degrees of change (or lack thereof), and sometimes this is information enough, but rates are something else again. We return to this topic again below.

Testing for Punctuated Equilibrium

The punctuated equilibrium theory and fossil data. The punctuated equilibrium theory (Eldredge and Gould 1972) claims that most morphological evolution is associated with cladogenesis. It is my intention in the following sections to discuss the punctuational hypothesis in the context of paleontological data on phenotypic change, typically within single geological sections. I shall demonstrate that most claims of supportive data ignore completely the most fundamental limitations of fossil data – namely, the equivalence of taxonomic rank and morphological difference. I shall also show that such change as has been documented can easily be accommodated into a scheme involving phyletic change within populations. This is not to say that cladogenesis has never occurred or that speciation is not occasionally or even often correlated with periods of rapid morphological evolution.

Punctuation and two definitions of *stasis*. The punctuated equilibrium theory is a claim at once about paleontological data and about the nature of speciation. Two principal assertions are made about the fossil record. First, the history of a species is dominated by stasis; change throughout the lifetime of the species is usually minimal and rarely directional (Eldredge and Gould 1972). The hypothesis also claims that speciation is the major source of phenotypic evolution, because phyletic evolution is too sluggish to generate sufficient change (Stanley 1979). Change, when it occurs, is therefore concentrated at times of speciation. Thus, evolution, as documented by the fossil record, consists of long-term periods of phenotypic equilibrium, punctuated by speciation events when form changes rapidly. Long-term stasis, especially when expressed as a lack of directionality (Schindel 1982b), is consistent with expectations of theoretical population genetics and could be accounted for by stabilizing and fluctuating directional selection. Organism-controlled patterns of habitat selection would reinforce stasis by keeping the progeny of each successive generation in approximately the same habitat. Overall constancy of habitat, habitat loyalty, plus culling of extremes, would explain stasis. Frequent broad ecological tolerance of single phenotypes would also result in stasis.

Discussion of the punctuational hypothesis has been confused because of the failure to distinguish between the claim, on the one hand, that evolutionary change in characters through a geological section is usually minimal – which I call *character stasis* – and, on the other, that evolutionary change is minimal because speciation is required for significant departures from the typical morphology to occur – which I term *species stasis*. *Character stasis* means simply the condition where for a given morphological character, no temporal change occurs. *Species stasis* implies that morphological change does not usually occur without a speciation event. This same distinction is made between the punctuational *pattern* (= character stasis) and the punctuated equilibrium *theory* (= species stasis). Some fine statistical analyses (e.g., Bookstein et al. 1978; Charlesworth 1984a) usually speak to the issue of character stasis but not to species stasis, and most of the consideration of fossil data, particularly in Gould and Eldredge (1977), also centers around the issue of character stasis and not species stasis. To deal with species stasis, one must have evidence that speciation has occurred in the lineage within which character change is measured. This is one case in which the fossil record fails the punctuated equilibrium theory. The theory also extrapolates into a known body of evidence that clearly shows extensive transitional evolution.

The punctuated equilibrium theory is, ironically, much more difficult to test than the alternative that transitions of the level of typical interspecies differences evolve anagenetically and commonly. To support punctuated equilibrium, you must have the entire history of the species. Stasis may be data, but anagenetic transformation from one "species" to another might occur in a short period of time, which is entirely compatible with population genetic principles. Either a bottleneck of population size, causing genetic drift, or selection could cause such a pattern. Alternatively, a transitional shift between ancestral and descendant taxa with no cladogenesis might be found by looking in sections where environmental change is likely to cause major morphological change by means of selection. Basin deepening is an obvious selective pressure, and transitional responses have been found at the interspecific and even intergeneric levels (Fortey and Owens 1990a; Miyazaki and Mickevich 1982; Nehm and Geary 1994; Sheldon 1987).

Can fossil species be identified, and what does the identification mean? There are many co-occurring species in fossil assemblages. In both vertebrate and invertebrate communities, quite stereotyped assemblages are found to be constant ecologically and taxonomically over many millions of years (e.g., Boucot 1975, 1983). Two questions must be raised:

1. Can we investigate cladogenesis among fossils at the species level successfully?
2. How are paleontological species usually recognized?

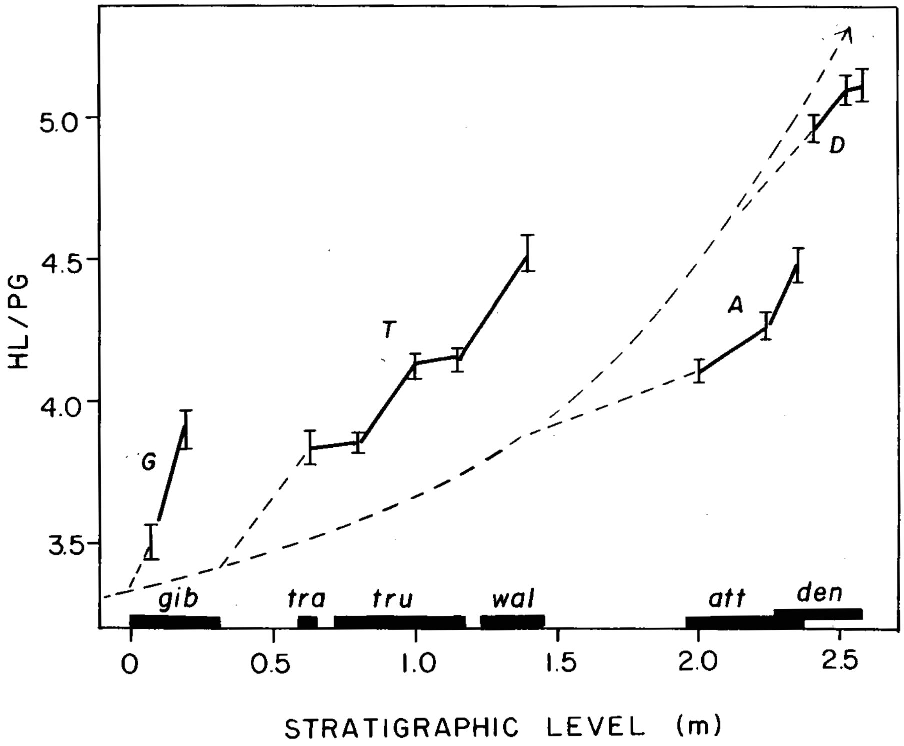


Figure 6.13. An inferred phylogeny within the Upper Cambrian trilobite *Olenus*. Four distinct iterative lineages, G, T, A, and D, were defined on the basis of several characters (illustrated here as a function of the ratio of head length, HL, to preglabellar length, PG). Within each lineage, a series of horizons (more than those depicted here) define transitions from one "species" to another (indicated by black bars at base). A conservative stock is believed to give rise to the lineages, and migration from a locale east of Sweden is believed to be the source. (After Kaufmann 1933.)

Even though we can see the outcome of cladogenesis, sometimes at small scales, the speciation events themselves usually fall through the cracks of the record. Fisher and others (1964) documented the evolution of the volutid gastropod genus *Athleta* and showed that a main stem stock is accompanied by several offshoots. Despite fairly careful sampling, they were unable to provide any real evidence on the time or exact phylogenetic pattern of cladogenesis. Kaufmann's[1] (1933) classic study of the Cambrian trilobite *Olenus* in Sweden identified four lineages or successions of taxa of species level rank. Each succession is distinct and demonstrates transitions from one "species" to the next (Figure 6.13), but an ancestral conservative stock, which supposedly gave rise to the four lineages, is only hypothetical. The progenitor stock may have been geographically remote and may have arrived in a chance immigration event

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[1] Owing to Rudolph Kaufmann's part-Jewish ancestry, Kaufmann's career was ruined by the Nazis. He was forced from his job and, after emigrating to Lithuania, was recognized by Nazi soldiers and murdered (Teichert 1946). Had he lived, he would probably have been a major paleontological contributor to evolutionary theory.

(Jeletzky 1955; Kaufmann 1933; Palmer 1984). Few paleontologists believe that entire paleontological populations evolve gradually into descendant states throughout the range of the taxon (but see evidence in Hallam 1982). On the contrary, the geographically peripheral origin of new taxa is widely given as the explanation for apparent sudden appearances in the fossil record. The findings of the lineage studies of Fisher and others, and of Kaufmann, are typical of the fossil record in general. Its generally spotty preservation usually precludes complete records of splitting. The previous discussion of temporal stratigraphic completeness suggests why this might be so.

When cladogenesis cannot be documented in the rocks, then it is unclear how it is possible to understand the relationship between speciation and morphological change in fossil lineages. A few studies have been able to document cladogenesis, and these are concentrated principally in mammals and open-ocean plankton (Tables 6.1 and 6.2). Gingerich's study of mammalian phyletic evolution (1976) shows an apparent split, but it is unclear whether this results from in situ evolution or, more likely, from immigration, because Gingerich was sampling from a single

Table 6.1. Examples of Gradual Change at the Intraspecific Level in Some Fossil Lineages

Taxonomic Group	Age	Character	Source
Fusilinid – *Lepidolina multiseptata*	Permian	Proloculus diameter	Ozawa 1975
Foraminifera – *Afrobolivina afra*	Cretaceous	Megalospheric proloculus	Reyment 1982b
Bivalve – *Nuculites planites*	Ordovician	Presence of anterior fold	Bretsky and Bretsky 1976
Bivalve – *Arisaigia postornata*	Silurian	Rib number, presence of ornament	Bambach 1970
Bivalve – various species	Miocene	Shell shape	Muller, Geary, Magyar 1999
Bivalve – *Cryptopecten vesiculosus*	Pliocene–Recent	Ornament	Hayami 1973
Ammonite – *Bullatimorphites*	Middle Jurassic	Various	Courville, Thierry, and Carious 1999
Ammonite – *Kosmoceras*	Jurassic	Size, shape, ornament	Raup and Crick 1981
Ostracode – *Cytherelloidea*	Cretaceous	Surface ornament	Bettenstaedt 1958
Trilobite – *Flexicalymene*	Ordovician	Axial rings	Cisne et al. 1980b
Fish – *Gasterosteus doryssus*	Miocene	Several	Bell et al. 1985
Mammal – *Microtus pyrenaicus*	Pleistocene	Dental characters	Brunet-Lecomte, Thouy, and Chaline 1994
Mammal – *Felis issiodorensis*	Pleistocene	Postcarnassial element	Kurtén 1963

Table 6.2. Some Cases of Gradual Evolution at the Transspecific and Transgeneric Levels

Taxonomic Group	Transition	Age	Source
Coccolithiphorids	*Chiasmolithus–Sullivania*	Paleocene	Bralower and Parrow 1996
Foraminifera	*Gaudyrina–Spiroplectinata*	Aptian–Albian	Grabert 1959
Foraminifera	*Globorotalia* spp.	Pliocene–Pleistocene	Malmgren et al. 1983
Foraminifera	*Bolivenoides* spp.	Cretaceous	Bettenstaedt 1958
Foraminifera	*Globoconella* spp.	Neogene	Schneider and Kennett 1996
Foraminifera	*Sphaeroidinellopsis–Sphaeroidinella*	Neogene	Malmgren, Kucera, and Ekman 1996
Radiolarians	*Pseudocubus* spp.	Pleistocene–Recent	Kellogg 1975
Bivalves	*Chesapecten*	Miocene–Pleistocene	Miyazaki and Mickevich 1982
Bivalves	*Pleurocardia subcurtum–P. pauperculum*	Cretaceous	Geary 1987
Bivalves	*Gryphaea*	Jurassic	Hallam 1982
Gastropods	*Melanopsis caryota–M. cylindrica*	Pontian	Staley 1992, cited in Geary 1995
Gastropods	*Prunum coniforme–P. christineladdae*	Miocene–Pliocene	Nehm and Geary 1994
Ammonites	Various interspecies transitions, in four familial/subfamilial lineages	Middle Jurassic	Bayer and McGhee 1984
Brachiopods	*Pentamerus oblongus–P. subrectus*	Silurian	Johnson and Colville 1982
Ostracodes	*Oertliella* interspecies transition	Cretaceous	Reyment 1982b
Trilobites	Six interspecies transition series	Early–Middle Paleozoic	Fortey and Owens 1990a
Trilobites	*Triarthrus* interspecies transition	Ordovician	Cisne et al. 1980a
Trilobites	Eight interspecies transitions, one generic	Ordovician	Sheldon 1987
Crinoids	*Calceolispongia* spp.	Permian	Teichert 1949
Graptolites	*Holmograptus–Nicolsongraptus*	Ordovician	Skevington 1967
Mammals	*Ursus* spp.	Pleistocene	Kurtén 1959
Mammals	*Lynx* spp.	Pleistocene	Werdelin 1981
Mammals	*Hyopsodus* spp.	Eocene	Gingerich 1976
Mammals	*Cantius–Copelemur*	Paleocene–Eocene	O'Leary, unpublished, 1999
Mammals	*Nyanzachoerus–Notochoerus*	Pliocene–Pleistocene	Harris and White 1979

(continued)

Table 6.2 ***(continued)***

Taxonomic Group	Transition	Age	Source
Mammals	*Tetonius–Pseudotetonius*	Eocene	Rose and Bown 1984
Mammals	*Mimomys* spp.	Pliocene–Pleistocene	Chaline and Laurin 1986
Mammals	Moose, *Alces* (four successional species)	Pleistocene	Lister 1993
Mammals	*Mimomys occitanus–ostramosensis*	Pleistocene	Viriot, Chaline, Schaaf 1990
Mammals	*Mammuthus* (four successional species)	Pleistocene	Lister 1993

section. Grabert (1959) and Prothero and Lazarus (1980) documented the splitting of lineages among foraminifers. Grabert found (Figure 6.14) increased intrapopulation variation at the time of splitting.

A quite similar pattern was found in the Miocene–Pliocene Caribbean marine gastropod *Prunum*, where a gradually changing (at least in a discriminant function axis score) lineage becomes quite variable and then appears to diverge into two descendants, including a morphologically distinct species (Nehm and Geary 1994). Geary (1995) saw this sequence as just a reflection of gradual evolution and variable rates of morphological change. The speciation event is effectively a range extension of a descendant species into deeper water; the colonization is accompanied by an expected amount of directional selection in the descendant species. The ancestral progenitor of the deep-water colonist actually continues to change gradually during and after the speciation event.

Can the punctuated equilibrium theory be tested when no splitting of a lineage occurs? Paleontologists have long worried about the problem of demarcation of species-rank taxa when an uninterrupted record of ancestors and descendants might occur (e.g., Newell 1947; Simpson 1944). Levinton and Simon (1980) pointed out the inevitable tautology established between species recognition and assessments of character change. Paleontological data are used to recognize speciation by identifying changes in "species-specific characters" (Eldredge 1974). Thus, morphological evolution can readily be related to speciation because one is the source of the other's inference! Successional sequences of "species" can be related to the molding of developmental patterns (McNamara 1982), but these sequences are geographical or temporal successions of forms without any evidence for cladogenesis; the recognition of species again required a definitional association with morphological differences. It is one thing to decide that it is necessary to use phenetic differences as a convenience to recognize fossil species, as in stratophenetic approaches (Bretsky 1979; Gingerich 1979). It is quite another to relate such changes to a qualitative process such as speciation.

It is instructive to look back at the first known example of a small-scale paleontological study inferring evolutionary relationships, for it sets the stage for the prob-

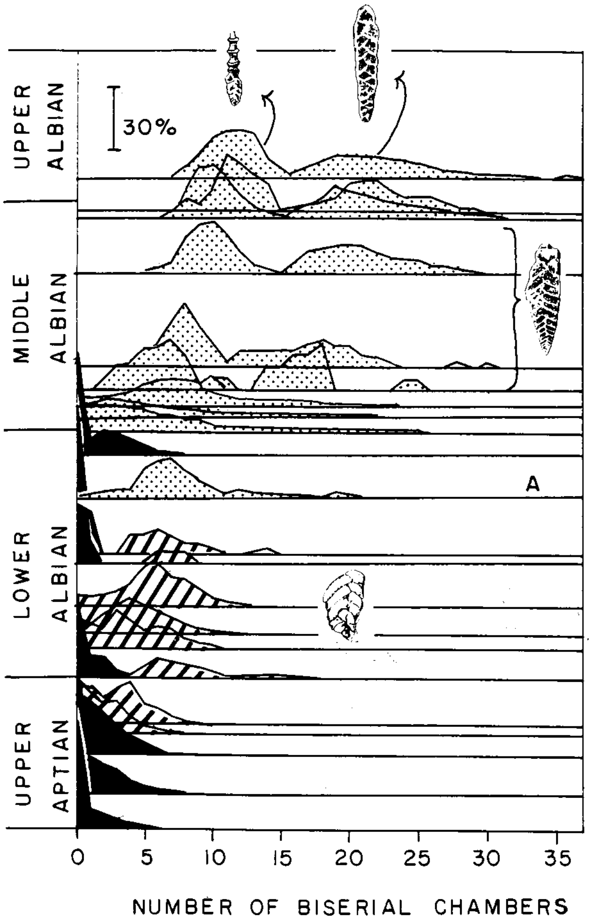


Figure 6.14. Transgeneric evolution between the foraminifers *Gaudyrina* and *Spiroplectinata* (black and diagonal stripes; intergeneric transition occurs at level A). Cladogenesis is inferred to lead to the evolution of *S. annectens* (pictured at upper left) and *S. bettenstaedti* (upper right) in the upper horizons. (After Grabert 1959.)

lems in the naming of species and in the analysis of splitting that have confronted paleontologists ever since. In the 1860s and 1870s, Hilgendorf produced the first Darwin-inspired phylogeny (Lamarck had inferred a phylogeny long before) of a planorbid species group (Gastropoda) from a Miocene freshwater lake deposit in the Steinheim basin of south Germany (see Lindenberg and Mensink 1979; Reif 1983a, 1983b and references therein). This case comes from a lake with a minor endemic evolutionary radiation. Hilgendorf described his taxa as varieties, or subspecies, and showed the phylogeny by gluing representative specimens onto cards, which were rediscovered by Dr. W.-E. Reif. Hilgendorf's inference of transmutation first derived from his observation that in the portentously named *Valvata multiformis,* flat forms always occupied the low part, and trochiform shells the high part, of the geological section. He used overall similarity of morphs between proximate strata (i.e., the "modern" stratophenetics of Gingerich 1976) to construct a phylogeny (Figure 6.15), which involved an "intergeneric" transition with no cladogenesis. His diagram included instances of splitting as well, and he even suggested a possible case of between-lineage fusion (i.e., hybridization). Overall, the 19 taxa he named arose from a combination of phyletic transformation and splitting, though the latter was less important. He noticed that change between successional species was relatively rapid, relative to longer periods of little change (Hilgendorf 1879 cited in Reif 1983a). Apparently, the claim by punctuativists that stasis is the rule for fossil species has a rather venerable history.

Hilgendorf adopted a compromise position on the taxonomic delineation of species (Reif 1983b). He believed that neither all morphs bridged by transitions should be assigned to the same species nor that all differentiable morphs should be

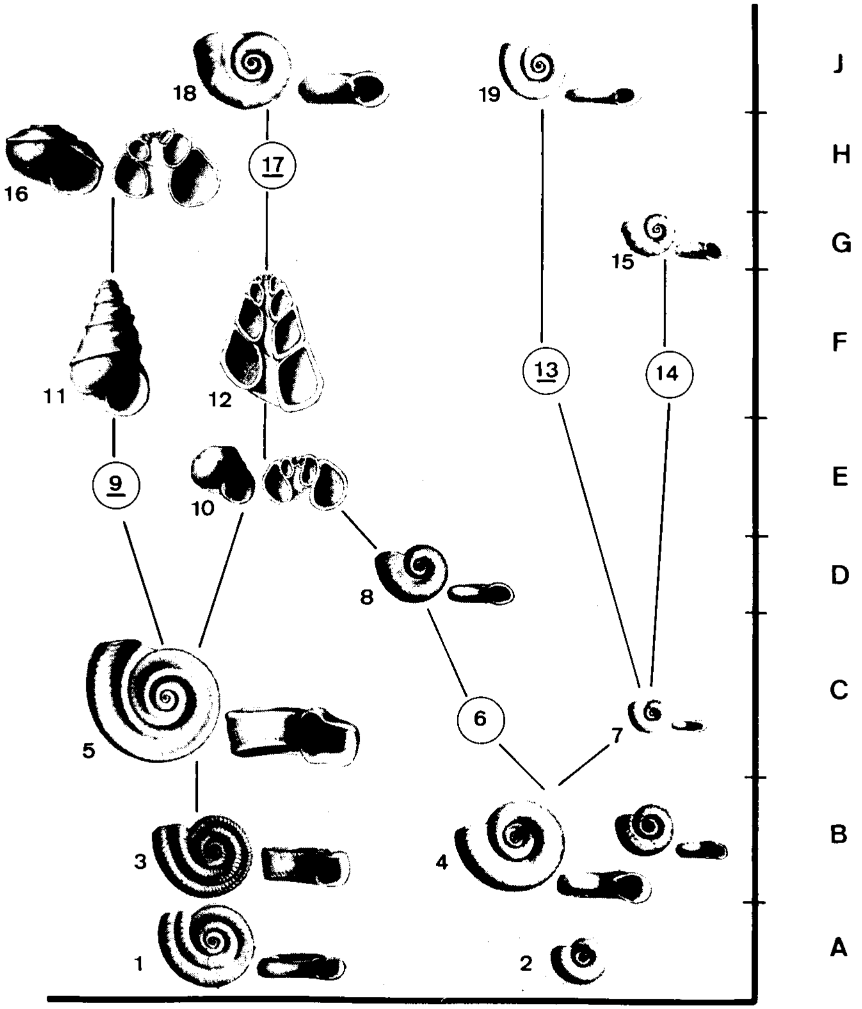


Figure 6.15. Reconstructed phylogenetic diagram for the *Planorbis multiformis* lineage, taken from Hilgendorf's 1863 thesis. (From Reif 1983a, with permission.)

given different species names. He chose qualitatively established thresholds of difference to assign species names. This method, of course, is precisely the same one used subsequently by nearly all paleontological systematists. It helps when the rate of evolution is uneven and breaks in morphological resemblance can be related to stratigraphic horizons. Thus, Hallam (1982, p. 358) argued from his experience with *Gryphaea*: "morphological trends concerning more than two species ... may be the expression of a simple one-to-one ancestor–descendant relationship." From the time of Hilgendorf to the present, paleontologists have demonstrated again and again that differences characteristic of coexisting species can be traced by phyletic change through geological sections. This is the most elegant refutation of the punctuated equilibrium argument, which claims that most species-level differences require cladogenesis.

The struggle to identify sibling species is well known, and one can only admire the many times neontologists have found extremely subtle characters that denote reproductive isolation. Perhaps the most sophisticated cases involve DNA-based studies (Avise 1994), which are beyond application in fossil cases, at least for the present. It seems strange that paleontologists would aggressively defend the notion that species could be identified with certainty in the fossil record, when surprises arise constantly, even in fossil cases. For example, Norris, Corfield, and Cartlidge (1996) noted that a fohsellid globorotalid foraminiferan displays a complete and subtle series of anagenetically intergraded forms. But isotopic analyses demonstrate a sudden change of depth of reproduction and that there are "...no correlations between anagenesis in skeletal shape and the establishment of reproductive isolation." Here, where a particularly clever new discovery of speciation occurs, we at once see the irrelevance of speciation to morphological evolution and also the tremendous hidden numbers of species that we have yet to encounter. There is no particular reason to believe that the finding of more species will of necessity yield more stasis, unless we eventually discover that speciation is more frequent than episodes of anagenetic change. If so, it is then still irrelevant to the issue of punctuated equilibria.

Testing character stasis and refutations of the punctuated equilibrium theory. Cladogenesis must be recognized before one can produce data consistent with the punctuated equilibrium theory. To falsify the punctuational hypothesis, an extrapolation of phyletic character change must be typically large enough to diagnose populations at two horizons as being members of the same phyletic evolutionary lineage yet belonging to different phenetic species (Gingerich 1976). Rapid changes in the rate of character change in a radiolarian (Gould and Eldredge 1977 – interpretation of data reported by Kellogg 1975) supposedly supports the punctuated equilibrium theory. As one moves up the stratigraphic column, phenotypic changes occur, with short periods of character stasis. It is rather unlikely that any character would change at a constant rate for millions of years, given variation in the rate of environmental change, possible (but unlikely) exhaustion of genetic variability, and stochastic processes. But this is precisely the trap that Eldredge and Gould have created for "gradualists." Must gradualists believe that evolution involves sustained evolution at a constant rate? Must mice evolve to be the size of Irish elks? Must euglenas evolve to be the size of Douglas firs? The absurdity of this reveals a clever trick used in rhetoric, to demonize the opposition by defining them in your own inaccurate terms.

Thus, to refute the punctuated equilibrium theory, gradual character evolution should be redefined: A character's evolution is *gradual at the species level* when change up a geological section is sufficiently directional such that reversals and periods of character stasis do not preclude phyletic divergence of two morphs sufficiently different to be recognized as distinct species. (Note: for the purposes of testing the potential of gradual evolution, we accept the diagnosis of species differences with a predefined threshold of phenetic difference.) In characters with discrete states, the distinction between gradualism and stasis-punctuation is indeterminate unless one knows the genetic-ecological basis of character-state determination. With this more reasonable definition, gradual evolution at the species level is a commonplace phenomenon in the fossil record.

Most studies by paleontologists in recent years have concentrated on one character in a single species (e.g., Hayami 1973; Kellogg 1975). It would be more valuable to study groups of species changing in the same geological section (e.g., Geary 1995; Sheldon 1993; Williamson 1981) and to consider a number of characters for each species (e.g., Bell et al. 1985; Brande 1979; Malmgren et al. 1983; Reyment 1982a, 1982b; Stanley and Yang 1987). It would also be desirable to measure character variability. Some hypothetical results would be illuminating in assessing the punctuated equilibrium theory. First, consider the case of discordant patterns of change occurring among characters within the same species. Suppose (Figure 6.16) that character A changes gradually with a constant rate of change, character B shows no change, and character C exhibits periods of character stasis, interrupted by rapid periods of change from one discrete state to another. Given such data, one can con-

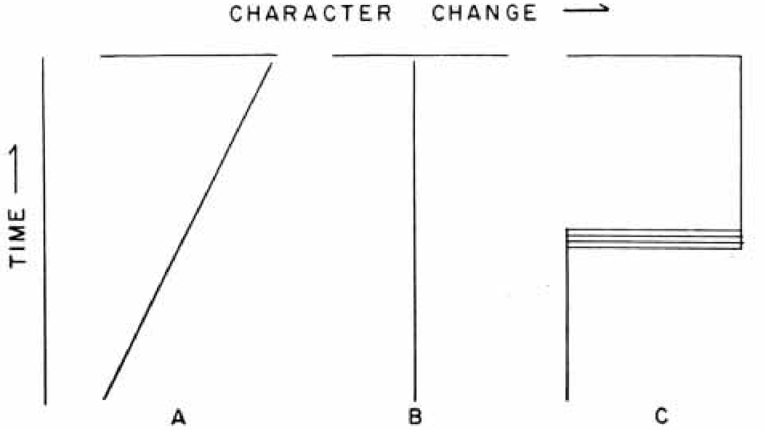


Figure 6.16. Different possible forms of character change through time in a fossil lineage: (**A**) gradual change in a character such as a linear dimension; (**B**) character stasis; (**C**) change from dominance by one discrete state to dominance by an alternative. The horizontal lines represent a period of polymorphism.

clude that no homogeneous process determines the mechanism of character evolution for all characters. Differing patterns of change might be explained by the following: (1) The genetic mechanism of character state determination differs among characters. (2) Either different characters may respond differently to the same selective agent or the characters may be influenced by alternative selection agents in the same overall environment. Such cases occur commonly in geographic variation of morphology and of allozymes (chapter 3).

In the Cretaceous foraminiferan *Afrobolovina afra,* megalospheric prolocular size changes steadily, but microspheric prolocular size is invariant (Reyment 1982b). In the same species, three discrete ornamental variants can be found as a polymorphism (Reyment 1982c). Similarly, Bambach's (1970) study of evolution in the Silurian bivalve *Arisaigia postornata* shows discordant patterns of change in different types of shell surface characters.

Michael Bell and colleagues (Bell and Haglund 1982; Bell. et al. 1985) examined the pattern of character change in a fossil stickleback. *Gasterosteus doryssus* is preserved in the Miocene saline Lake Truckee and can be collected from diatomites layered in annual varves, over an inferred and stratigraphically complete period of 110,000 years. The characters he investigated – pelvic structure, predorsal pterygiophore number, dorsal spine, dorsal fin ray, and anal fin ray number – are all known to have a strong genetic component of variation in the extant species, *Gasterosteus aculeatus*. The various characters have different mechanisms of genetic determination, which partially explains the different patterns of change (Figure 6.17). Known effects of ecophenotypic changes in the environmental factors on morphology of modern species cannot explain the degree of evolutionary change in *G. doryssus*. In all characters, gradual evolution is predominant; it is nearly linear in one character (Bell et al. 1985). In some cases, the changes would represent those diagnostic of family-level differences in teleosts. Rapid evolutionary bursts are seen, but the most rapid change most likely represents a local extinction, followed by immigration from another differentiated population. The patterns of change indicate that conventional paleontological samples, which usually record changes of far greater temporal magnitude than the common case here of 5,000 to 10,000 years, must usually be too widely spaced to pick up much significant evolutionary change.

This discussion highlights the inherent difficulty of understanding the mechanisms of character stasis or gradual change by using the fossil record. We do not know the mechanism of genetic determination of character states, and we cannot predict the norms of character reaction to the environment without genetic–environmental data. Genetic mechanisms behind fossil variation are difficult to infer, and Mendelian variation has almost never been found. (See Best 1961 for an interesting example in trilobites.) When "sudden" and qualitative changes, such as in surface shell ornamentation, are found (e.g., Hayami 1973 – intraspecific case; Reyment 1982c and Skevington 1967 – transspecific examples) they can readily be related to characters that are probably determined by polygenic systems with threshold effects. Invariably, a polymorphism is observed, documenting the transition from dominance by one morph to the other. For example, consider the reticulation that appears rather suddenly as a new phenotype in the Cretaceous ostracod *Oertliella*

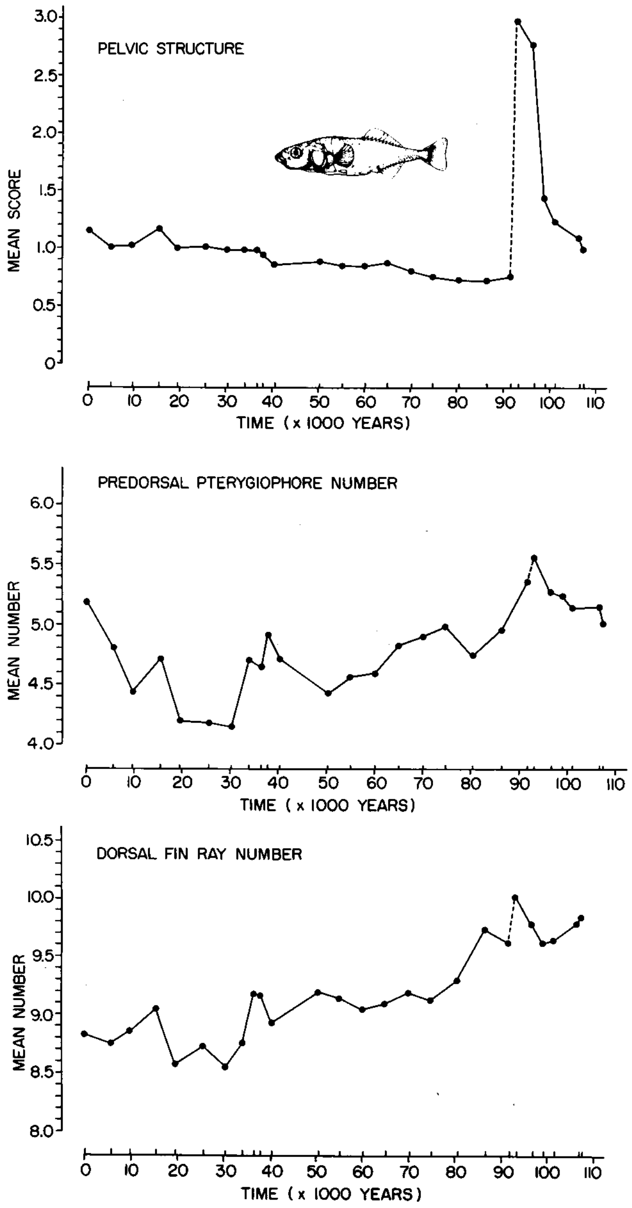


Figure 6.17. Temporal changes in three characters in the Miocene stickleback, *Gasterosteus doryssus,* in fossil Lake Truckee. Time control established by varves. (From Bell et al. 1985, with permission.)

(Reyment 1982a). Such ornamentation (Figure 6.18) can be easily "switched on," as it probably is controlled by a set of underlying epidermal cells that can be signalled simultaneously to control skeletal morphology (Okada 1981). The polymorphism for reticulation in *Oertliella* species could easily be the effect of a single gene. There are other differences between the two species, but intermediate "passage" forms for

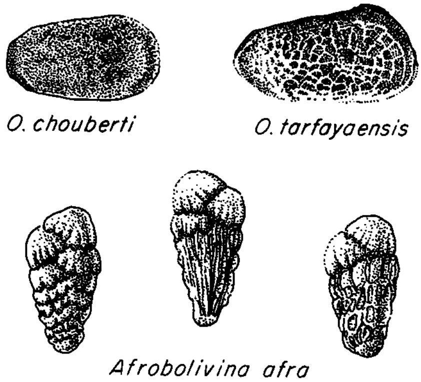


Figure 6.18. Examples of discrete morphs in fossil lineages. Top: The Cretaceous ostracodes *Oertliella chouberti* and *O. tarfayaensis* (female carapace, right side). Although these are described as different species, they are members of a single phyletic lineage, and passage forms have been identified. The derived *O. chouberti* does have features lacking in the ancestral species. (After Reyment 1982a.) Bottom: Three discrete morphs coexisting in populations of the Cretaceous foraminifer *Afrobolivina afra.* (After Reyment 1982c.)

all characters have been found (Reyment 1982a). The derived form arises in a confined geographic area, relative to the ancestral form, so there can be little doubt that one "species" evolved into another. In a more recent study of a similar ostracod system, Reyment (1985) found similar arrays of morphology, but with far more cases of intermediate forms. It is likely that the same transition was selected but that a different mechanism of genetic determination with fewer threshold effects altered the character of evolutionary change. This only points to the variety of mechanisms of genetic determination of traits and the futility of pointing to specific character changes as examples of punctuation. Jackson and Cheetham (1999) fell into this trap by pointing out cases of stasis and apparent punctuation without considering genetic determination of character states.

The original case cited (Eldredge 1971) for punctuation – a "sudden" change in file number (number of rows of eye facets) in the American Devonian trilobite *Phacops rana* – could be simply based on a transient polymorphism controlled by minor thresholds known to occur in living arthropod populations. One would be hard pressed even to demonstrate that this was a speciation event, as claimed by Eldredge. The geographically peripheral origin and subsequent spread of a variant is hardly a unique element of speciation; it is the expectable outcome of within-species evolution. No one expects variants to arise *and* be fixed simultaneously throughout the range of a species. But given that a fixation event is likely to be missed and that spread is likely to be rapid, most fossil cases will appear to demonstrate such an unlikely event. Could the fossil record have documented the spread of the melanic morph in the pepper moth *Biston betularia* through most of its range in a century?

One might take the peculiar position that transitional change, seen so beautifully in many studies of oceanic protistans, is just qualitatively different from other groups (forgetting for the moment that other groups show rampant transitional change as well). Prothero (1992) found himself in this trap. "Perhaps much of the morphological change seen in microfossils does not reflect any underlying genetic change, but is simply an ecophenotypic response to the changing environment..." (Prothero 1992). He apparently thought that foraminifera simply are not the same kind of thing as monkeys or fiddler crabs. Although he was correct in emphasizing the differences of oceanic species from those with more isolated and tiny populations, like direct-developing snails in estuaries (Seeley 1986; Vermeij 1982) and mice in isolated mountain valleys (Capanna 1982), he forgot the enormous number of species, ranging from copepods to jellyfish to tunas, that are more or less in the same boat as forams, with widespread and large populations. His argument that morphological variation in planktonic foraminifera is different, mainly ecophenotypic, has the strength of our current ignorance; we don't have a lot of data on genetic variation in foram planktonic traits. (We do know, however, of cases of distinct foraminiferal polymorphisms, as mentioned above.) But then again, that turns out to be true for most of the traits that have been examined in fossil lineages and most of the traits we measure in living creatures. The claim is more assertive than substantive. In any event, the nature of phenotypic expression of traits is itself genetically determined and plasticity of expression is found widely in animals and plants.

The confusion about punctuation and character change is exacerbated, as many paleontologists use sudden changes in character state as opportunities to delineate species. For example, external ornamentation in the Cretaceous foraminiferan *Afrobolivina afra* occurs in three discrete morphs (Figure 6.18), yet the documentation of these forms is not evidence for punctuation, as polymorphism is found and the morphs are most likely determined by standard genetic mechanisms (Reyment 1982a). If the morphs occurred in three geographically discrete populations or in successive horizons, it is certain that there would be three named "species" of *Afrobolivina* instead of just one. Newell's (1947) quote from another paleontologist, F. W. Millet, is perhaps an exaggeration of typical practice, but it is often close to the truth:

> In preparing your slides you should be very careful to select typical specimens only, the intermediate things are a nuisance and should be severely ignored, unless the types are absent from the deposit. . . . Take *Globigerina,* the difference between *G. cretacea* and *G. lineana* is very great, but you can select specimens that will form a complete chain from one to the other.

Recognition of this problem is not very new. Meyer (1878) claimed that the ability to recognize gradual evolutionary change in *Micraster* was obscured by the rampant naming of separate species by previous taxonomists.

Periods of character stasis, strong variations in the rate of character evolution, and the appearance of new morphs controlled by easily attributable and trivial genetic mechanisms are the mainstay of species-level taxonomy in the fossil record. One could not easily delineate qualitatively different taxa without such breaks. But these apparently rapid changes are usually within single lineages with no observed cladogenesis. If apparent species-level differentiation can occur in such instances, then what does speciation have to do with phenotypic evolution? The punctuativists' typical test (e.g., Gould and Eldredge 1977) of the causal relationship of speciation to morphological divergence is usually dependent on the tautologous relationship of change with species taxonomy (Levinton and Simon 1980). Species-level and genus-level differences are also exaggerated, with no substantive support from the paleontological literature (see, for example, Rose and Bown 1984). Stanley (1979), for example, claimed that Bjorn Kurtén's work indicated substantial gaps among fossil mammal genera and species. But Kurtén (letter, October 21, 1981) replied: "I most certainly do not believe any such thing. I tend to regard genera as after-the-event artifacts. . . . I think new genera can arise rapidly or slowly. I think the same holds for species." Intergeneric differences in mammals can be shown to be rather slight and easy to document in fossil lineages (Figure 6.19). Splitting may sometimes increase the rate of species evolution because the wide spread of a population will cause it to encounter a wide variety of environments.

Teichert (1949, p. 49) revealed the paleontological practice of naming species tautologically by degree of morphological difference:

> Tan ... demonstrated how in Lepidocyclinidae the "variation curve of the same species gradually shifts in a definite direction." In *Calceolispongia* these shifts are so quick that assemblages in consecutive horizons are distinct enough to be separated species, although there is considerable overlap in morphological variants.

We see here the acknowledgment of morphological variation, but the inevitable tendency to name species when a threshold of mean phenetic difference is surpassed. Werdelin's (1981) study of the evolution of the felid genus *Lynx* is a typical example of how a phyletic series of species is eventually defined by a series of taxa, based on characters known to change rather easily in phyletic evolution and also known to be polymorphic. Figure 6.20 shows the inferred phylogeny, demonstrating a line of interspecific transitions. The genus *Lynx* itself is defined by the absence of the second premolar, a character state that reappears later within the group and is known to be polymorphic in several felid species. The multispecies transition in Europe

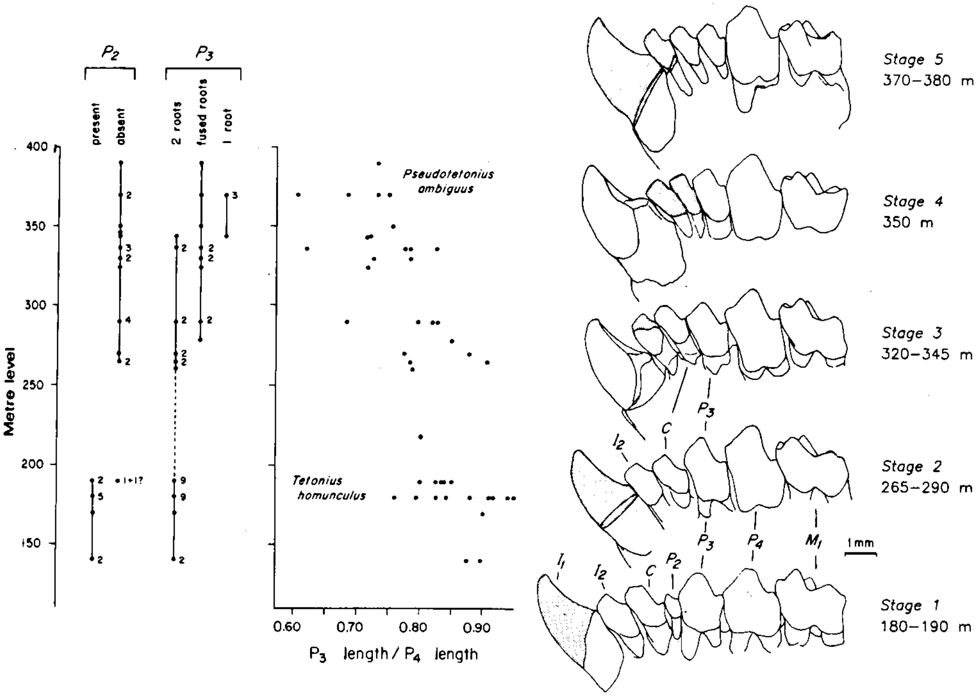


Figure 6.19. Evolution of the anterior lower dentition in the omomyid primates *Tetonius homunculus* → *Pseudotetonius ambiguus* lineage from the central and southern Bighorn Basin, Early Eocene. Shaded areas are reconstructed. (From Rose and Bown 1984, with permission.)

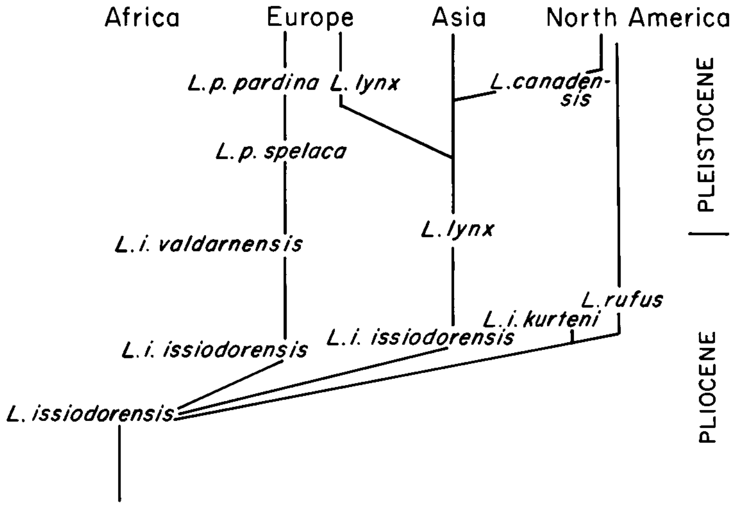


Figure 6.20. The phylogeny of the genus *Lynx*. Note the transitional subspecies and species in the evolution of *L. pardina*. (After Werdelin 1981.)

from *Lynx issiodorensis* to *L. pardina* is gradual, and species are defined principally on the basis of the relative length of the first molar, though gradual reduction in size also occurs. This pattern is the rule among mammals, where morphological change has been studied more completely than in any other group. Carroll (1997) carefully examined the literature and found that gradual (= transitional) change is the rule, not the exception, and explains many cases of successive anagenetic "species." He pointed out (p. 110) that speciation is associated only with major dispersal events, followed by isolation. Nevertheless, "...most morphological change occurred subsequent to the actual speciation event, in relationship to the new environment." This is not to say that there are no instances of character stasis; there are. Also, there are cases known where character change is correlated with times of cladogenesis, but ... so what? Many radiations are accompanied by rapid morphological divergence, which is ecologically driven. Although especially true of fish (e.g., Johns and Avise 1998; Meyer, Kocher, Basasibwaki, and Wilson 1990; Schluter 1993), rapid shifts are expected as a radiation occurs.

The confusion between species change and character change injects bias in searching for ordinary population genetic mechanisms of evolution in fossil lineages. Paleontologists are always looking for boundaries to which they can assign temporal significance. This is true for the *Sphaeroidinellopsis–Sphaeroidinella* lineage, a foraminiferal lineage that figures in tropical late Neogene stratigraphy. The appearance of the *Sphaeroidinella* morph, with a supplementary aperture on the spiral side of the test, marks the basal Pliocene Zone N19 (15.1 million years ago). But this morph had already appeared in the terminal Miocene (before 5.5 million years ago), although it remained in small frequencies (10% to 30%) until the intergeneric boundary. The proportion increased abruptly within a short interval (less than 0.1 million years, during the period 3.4 to 3.2 million years ago), and after 3.0 million years ago, more than 85% of the specimens had a supplementary aperture (Malmgren et al. 1996). This case demystifies change into the polymorphism expected to be found in living populations.

The case for gradual change. Gould and Eldredge's (1977) review and Stanley's monograph (1979) both suggest that there is little evidence of gradual evolution in fossils and that morphological evolution is generated by discrete speciation events. It is telling that Gould and Eldredge's more recent review could barely find more than a handful of new studies supporting, or purporting to support, punctuated equilibrium. Moreover, they cited a number of studies that already had been discounted except for showing stasis in a lineage. Stasis is data but not a demonstration of the predominance of punctuated equilibrium.

In contrast to Gould and Eldredge's claims (1977), the fossil record is full of excellent examples of gradual evolution at the intraspecific (Table 6.1) level. Continuous change in nondiscrete characters, or transitions in characters that are developmentally or genetically determined as discrete states, has been found in foraminiferans, radiolarians, ammonites, bivalves, ostracodes, trilobites, graptolites, echinoderms, mammals, and fishes. Indeed, the burden of proof is on those who claim that such evolution cannot be found or is even the minority case. When the evidence is pruned down to convincing cases, I would say that at best, one can infer punctuated equilibrium patterns as dominating the results of Jackson and Cheetham (1990) and a few cases in which expected high-tempo of speciation occurred in freshwater basins (e.g., Williamson 1981, part of Geary 1995; one of two clades).

Between-species boundaries in the stratigraphic column are, not too surprisingly, placed where evolutionary rate appears to have increased markedly (e.g., Malmgren et al. 1983) or where discrete changes occur in phenotypic traits that, by analogy to living populations, are likely to be determined by several genes with thresholds between states (e.g., Malmgren et al. 1996; Werdelin 1981). Transitional evolution has been documented in the absence of cladogenesis for transspecific (e.g., Kaufmann 1933; Malmgren et al. 1983; Chaline and Laurin 1986; Hallam 1982; Reyment 1982a, 1983b) and even transgeneric (Grabert 1959; Rose and Bown 1984; Skevington 1967) evolution (Table 6.2). Most important, variation within populations accounts for the differences observed between ancestral and derived taxa (see Charlesworth 1984a; Malmgren et al. 1983; Reyment 1982a). This is best seen in the works of Kurtén and his colleagues (e.g., Kurtén 1959a; Werdelin 1981). Within-species dental polymorphism is the stuff of transspecific diagnoses in mammals. Ironically, it is easier to find sources on transspecific evolution than on intraspecific evolution.

The marine protists are excellent for tests of hypotheses concerning character evolution and "species" origins. The deep-sea drilling program has greatly amplified an already large body of data. Gradual evolution, even by Eldredge and Gould's narrowly defined standards, seems common (Figures 6.21 and 6.22).

Kennett and Srinavasan's (1983) monograph on Neogene foraminifera demonstrates that interspecific phyletic evolution is commonplace. Recent studies (Kucera and Malmgren 1998; Lazarus, Hilbrecht, Spencer-Cervato, and Thierstein 1995; Malmgren and Kennett 1981; Malmgren et al. 1983; Prothero and Lazarus 1980;

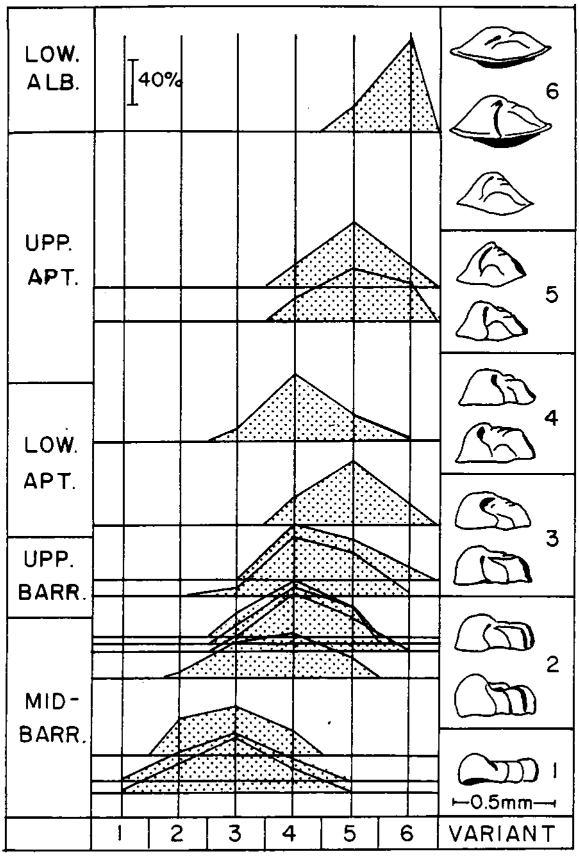


Figure 6.21. Gradual evolution of the Cretaceous foraminifer *Globorotalites bartensteini* from the Barremian to the Lower Albian. Several variants of the species (at right) coexisted at any one horizon. (After Bettenstaedt 1958.)

Reyment 1982b; Wei and Kennett 1988) have only duplicated the findings of the classic German works of the 1950s and 1960s (Bartenstein and Bettenstaedt 1962; Bettenstaedt 1958, 1959, 1960, 1962; Grabert 1959) and of earlier work in the 1930s (summarized in Tan 1939). These older studies estimated variation at a given geological horizon and found that changes in the frequency of morphs at any one horizon accounted for the changes across horizons and between successional species (Figures 6.21 and 6.22). Good stratigraphic sampling can help to explain generic-level transitions. One might argue that the foraminifera are biologically unique and hence not an adequate sample of evolutionary history. But the Mammalia fit this pattern as well. I would argue that foraminifera are exceptional solely from the point of view of sedimentary and geographical continuity.

An exceptional study of the radiolarian lineage *Pterocanium prismatium* shows the ambiguities that arise when complete sections are available (Lazarus 1986). The lineage gave rise to the distinct species *P. charybdeum* within an interval of 50,000 years at approximately 4.3 million years ago. Both descendants continued to diverge

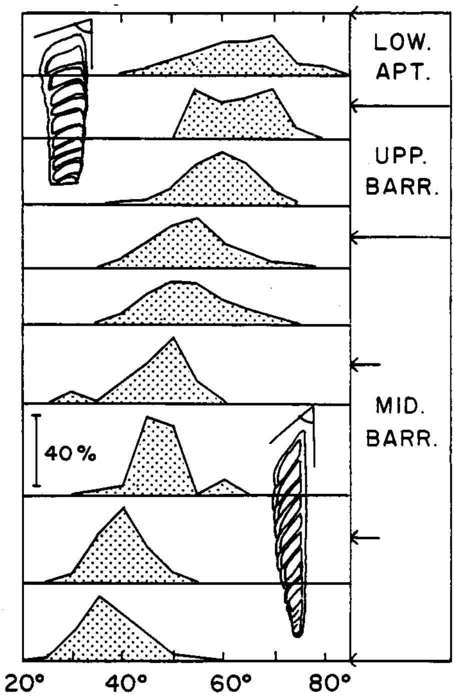


Figure 6.22. Gradual evolution in the angle between the chamber wall and the main body axis in the Cretaceous foraminifer *Vaginulina procera* from the Middle Barremian to the Lower Aptian. Arrows denote "interspecific" boundaries. (After Bettenstaedt 1962.)

over the next 0.5 million years, with over 10 standard deviations of difference accumulated. Over the next 2 million years, divergence slowed down considerably. This is hardly an example of punctuated equilibrium, but it would have been characterized as such if one of the daughters failed to change substantially. The split in this case was not the motor of morphological evolution. Divergence continued long after. If this is the case, why should the change of only one descendant be considered consistent with punctuated equilibrium unless we in fact know that the speciation event itself is the cause of change?

Although it is clear that foraminifera and smaller fossils such as ostracodes are amenable to detailed sampling, they also reveal some important factors that influence our perception of character evolution. Recent evidence demonstrates, for example, a number of cryptic species of foraminifera in Pliocene and Pleistocene oceanic cores. The silhouette of the *Globorotalia* (*Fohsella*) lineage fossils comprises a nearly unbroken anagenetic trend, yet temperature-related isotopic data show that the fohsellids changed their depth of reproduction during the anagenetic evolution of their skeletons. Thus, character evolution may have been slow and keyed into oceanographic changes, but speciation may have been sudden and unimportant to the evolutionary change. Speciation was apparently uncoupled from morphological evolution in fohsellids because these evolutionary phenomena occurred in different phases of ontogeny (Norris et al. 1996).

At this time, the case for transitional change at the species level is bolstered by the majority of studies. To be honest, I am surprised about this. One can find stasis over long intervals before rapid changes in morphology, but this is quite different than punctuated equilibrium, which requires splitting. It is telling that a summary table of cases of punctuated equilibrium (Erwin and Anstey 1995, Table 1.1) states [in the fine print at the bottom] that "...position in the table generally reflects the conclusions of the authors cited, and not subsequent debates." This is telling, as several studies were claimed to support punctuated equilibrium before it was pointed out that they merely supported irregular changes in rates of evolution or long-term stasis for some of the history of a lineage. Other studies (e.g., Kelley 1983) involve no cladogenesis, which means no possibility to even test punctuation. Even the original studies by Gould (gastropods) and Eldredge (trilobite file number), cited in Eldredge and Gould 1972, have been successfully attacked (Brown 1987). Erwin and Anstey showed that more cases of stasis can be found in lineages with more branching, but this may be an artifact of the shorter geological ranges of the species in frequently branching lineages, giving them less opportunity for anagenetic change.

In some cases, it is possible to associate environmental change with morphological change, but we know that such a relationship is not likely to be simple, even monotonic. The stratigraphic–environmental context of evolutionary change is crucial in attempts to establish such relationships. Small-scale transgressive–regressive cycles in shelf basins are common in the fossil record and relatively easy to document. Miyazaki and Mickevich (1982) demonstrated a morphological change in a nearly unbranched anagenetic succession of scallop "species" correlated functionally with deepening of the Miocene–Pliocene basin in the middle Atlantic United States. Bayer and McGhee (1984) multiplied this approach by documenting iterative cycles of morphological change in a Jurassic basin in southwestern Germany. These are correlated with a succession of transgressive–regressive sedimentary cycles through which ornamented, evolute, and complex-sutured shells give way to discoidal, involute, unornamented, and simple-sutured shells in several lineages. Some of this anagenetic transformation can be captured in changes in logarithmic spiral shell parameters S and D (Figure 6.23; see chapter 5). Successional species of trilobites with no cladogenesis demonstrate clear adaptive changes in eye development, ribbing, and other traits (Fortey and Owens 1990a).

Let me be clear about this: Even if an anagenetically connected string of "species" occurs with complete stasis for each species, this does *not* mean that punctuated equilibrium is supported. A succession of species with morphological change but no cladogenesis means transitional evolution. Such examples are rampant.

Unfortunately, the fossil record of plants seems not to have been studied with such stratigraphic care and may often be too poor in occurrences for adequate sampling. Although his sampling was sparse, Asama (1959, 1962, 1981) documented apparent phyletic evolution in a number of lineages of Carboniferous and Permian plants. For example, the Shansi flora of China can be sampled through a major change of environment recorded by transitions from Carboniferous marine carbonates to nonmarine Lower Permian coals, to nonmarine red sandstones, of possible Triassic age. A sequence of 33 beds has been sampled sequentially in the Shihhotse Valley of China (Asama 1981). Through these sequences, Asama documented the gradual evolution of simple leaves in several unrelated lineages, through enlarge-

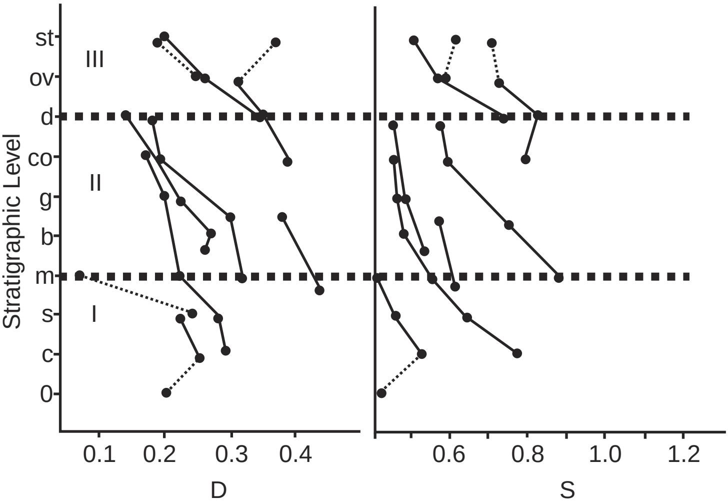
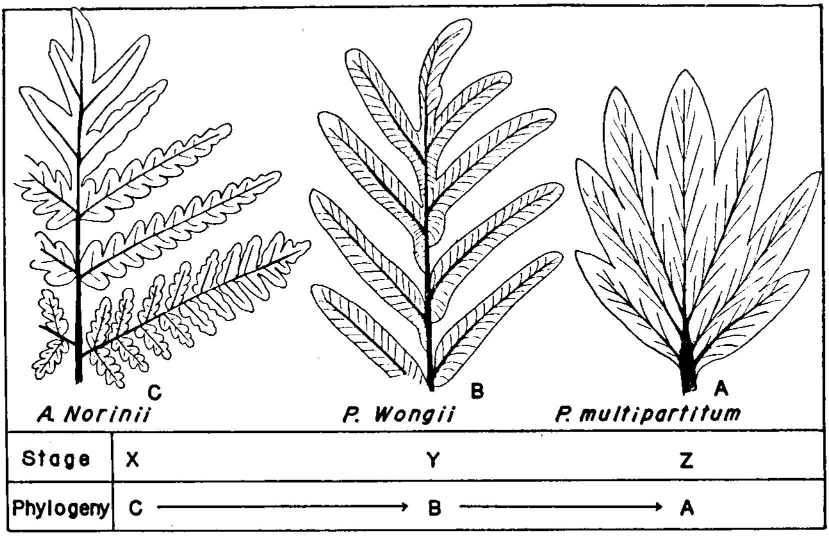


Figure 6.23. Temporal trends in mean *S* and *D* values for dominant south German Middle Jurassic ammonites. (Adapted from Bayer and McGhee 1984, with permission.) These and other changes document anagenetic species strings, where morphological changes are in response to cycles of regression (I, II, and III). See Figure 5.14 and related discussion for some explanation of characters measured.

ment, and through fusion achieved by growth retardation (Figure 6.24). Significant changes can be seen within a geological series (subsection of a period, such as the Permian). These changes are associated with overall drying trends in the environment (see also Wolfe and Hopkins 1967).



Stage	X	Y	Z
Phylogeny	C ⟶	B ⟶	A

Figure 6.24. Branching sequence and phylogeny in the transitional sequence *Alethopteris norinii* → *Protoblechnum wongii* → *Psygmophyllum multipartitum,* Permian of China. (From Asama 1962, with permission.)

Body size and Cope's rule. Edward Drinker Cope's rule, that body size tends to increase over evolutionary time, probably stands as the single most popularly known and possibly most accepted evolutionary dictum. Its role in evolutionary trends blends anagenetic and above-species-level trends. Springing from the time when the ideas of élan vital and orthogenesis dominated evolutionary thinking, Cope's rule fit well with the expectation that there were internal driving forces in evolution. But claims can often be right for the wrong reasons. Size increase is a major feature in the history of many fossil lineages. Many vertebrate lineages, from horses (Marsh 1879) to elephants (Osborn 1934) to dinosaurs (Sereno 1999), have body size increases enmeshed in their history, irrespective of the modernity of the investigator's point of view. Even if orthogenesis is long gone as an actively debated concept, it is still true that on average, younger lineages of fossil horses are larger in body size than older ones, just as Marsh argued from observations of his collections of fossil horses at Yale. What is not so simple is the course of this evolutionary track. As Simpson (1944, 1951) noted, horses comprise a complex set of evolutionary radiations, from which emerged the many temporal trends that have been long described, including size increase, toe simplification, and hypsodonty (MacFadden 1992).

Do not get bogged down in the simple question of whether size increase occurs without fail in all lineages. Quite simply, it does not: not for horses (MacFadden 1992) and not for other groups (Jablonski 1997a; Alroy 1998). Does bigger even mostly happen? If so, what is the exact pattern? Is bigger better? These are the useful questions still raised by Cope's rule.

Let's oversimplify and define two alternative ways that size might increase over time (Figure 6.25). First is the *size transformation model.* In a single lineage, an ancestor might appear and subsequently, size might increase monotonically, perhaps along with other characters, which in combination might be used to define successional species. Thus, later faunas would include uniformly larger species and smaller ones would have disappeared. This conforms to Cope's rule. Alternatively, in the *large taxon addition model,* an ancestral lineage might appear that is small in body size and persists for many millions of years. It may, however, split and proliferate larger descendants along with descendants of about the same diminutive size as that of the ancestor.[2]

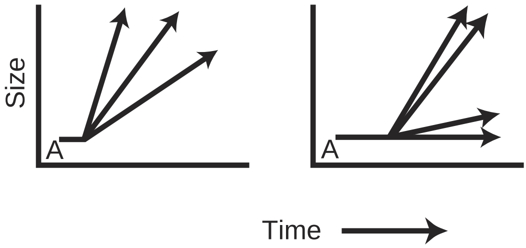


Figure 6.25. Two alternative means of obtaining a size increase in a clade. **(A)** A single ancestor gives rise to three descendant lineages; within each is a steady size increase. **(B)** An ancestor persists as lineages of about the same small size but gives rise to a set of distinctly larger descendant species.

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[2] Also, please do not get bogged down in whether the size changes are gradual or punctuational.

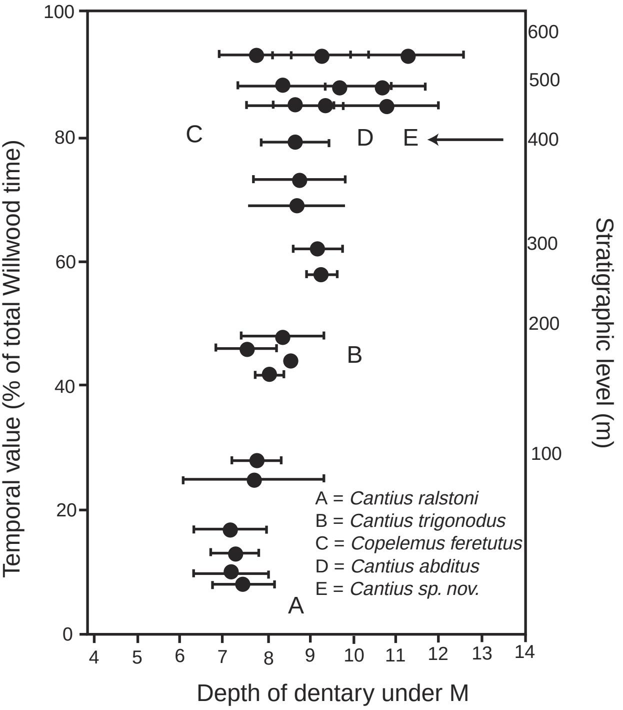

Figure 6.26. Temporal change in primate dental characters in the Willwood Formation. Gradual evolution involves several anagenetic species transitions and even a generic transition. (From O'Leary, unpublished data 1999, with permission.)

If for some reason a lineage is bound to begin with small body size, then it would be inevitable that larger species would appear in a subsequent time, conforming to the large taxon addition model (Stanley 1973). Small and simple form may be a common successful formula for surviving a crisis (Stanley 1973c). The two major Cenozoic radiations of planktonic foraminifera were initiated by small globose forms and were succeeded by small species along with larger-keeled forms (Cifelli 1969; Norris 1991). It is not clear whether the appearance of larger forms represents a pseudoextinction event with small lineages merely evolving anagenetically into large-size species or whether small species preferentially become extinct during the radiations (Arnold, Kelly, and Parker 1995).

Where lineages have been tracked, it is clear that evolutionary radiations often involve preferential size increase of ancestor-to-descendant anagenetic changes (horses, MacFadden 1992; mammals, Alroy 1998; birds, Maurer 1998; planktonic Foraminifera, Arnold et al. 1995). Reversals do occur within the broader trend of size increase (horses, MacFadden 1992 and Alberdi, Ovtiz-Jaureguizar, and Prado 1998).

The common increase we observe in size may have no unique explanation. Indeed, it appears that size is a surrogate for other factors. Mammals living in the Cretaceous were probably confined by intertaxon competition to microhabitats that were nocturnal and selected for only small body size. With the advent of the Cenozoic morphological diversification, dinosaurs were no longer around, and many open habitats selected for ecological diversification and larger body size. Open browsers, running hunters of larger prey, and swimming carnivores are just a few examples where large body size would be advantageous. Alroy (1998) made a convincing case that mammalian body size increase in the Cenozoic is layered on top of an extant suite of smaller mammals that do not change much in size. In the plankton, the rise of stable oceanic water columns might allow the greater occurrence of predators. The stable water, combined with predation, might select for larger, ornamented forams, which might sink more slowly from the water column and might better resist predators.

Sexual selection must certainly be a source of body size increase in many groups, particularly primates. Intermale competition, particularly in polygynous clades, is a driving force for greater armament and larger body size. Haplorhine species in more polygynous clades are significantly more dimorphic, have larger males, and also have larger females, but to a lesser degree (Lindenfors and Tullberg 1998). This suggests that sexual selection drags both male and female body size upward.

The evolution of horses, a classic example of Cope's rule, is a bit muddied by complexity. MacFadden (summarized in 1992) has convinced us that size does increase, although there are important cases of size decrease. In general, the appearance of open range grasses in the Miocene must have contributed to selection for larger open range grazers, which would supplant smaller browsers. The record of change is recorded not only in body size increase but also in hypsodont teeth and other features. Nevertheless, Pliocene horses still included browsers, as judged by carbon-isotope ratios corresponding to C3 plants (MacFadden, Solounias, and Cerling 1999). The overall pattern of size increase can therefore be considered only a net trend, even if there are many instances of size increase within lineages. It is entirely possible to have a period of no size increase at all, as Jablonski found for Maastrichtian bivalves and gastropods. Cope's rule is apparently intact, as long as you don't call it a rule! Call it a WHU (what happens usually).

Stasis

There is no contradiction in showing that (1) interspecific differentiation derived from intrapopulation variation is an entirely plausible explanation for evolutionary change and that (2) change of a phenetic-specific level does not always – in fact, usually does not – occur. Stasis may be the dominant pattern. For example, continuous gradational evolution has been claimed to be relatively rare in shelf invertebrates (Johnson 1982; Schindel 1982c). This may be explained by the strong association of benthic fossils, such as articulate brachiopods, with particular sedimentary and hydrological regimes. Benthic species often are diagnosable by sediment type (and rock type) and become locally extinct when the particular environment disappears. An apparently constant environment thus maintains an unchanging morphology. Abrupt changes in the environment of the shelf are associated with alteration in the sedimentary regime often too severe for a species to survive.

In his extensive studies of the invertebrate faunas of nearshore mid-Paleozoic deposits, Boucot (1975, 1978) provided an environmental description that indicates why morphology of many taxa should fluctuate but usually shows no directional change to any major degree. Community composition is remarkably constant over tens of millions of years in terms of both species composition and relative frequency of species. Even when specific taxa change, functional groups within Paleozoic shallow-water environments (Walker and Laporte 1970) and within Permian vertebrate communities (Olson 1966) often remain the same over long periods of time. Boucot suggested that such physical and biotic environmental constancy leaves little room for expectations of major directional evolutionary changes. In Late Devonian nearshore marine communities dominated by brachiopods, extinctions of dominant elements usually were followed by replacements by morphologically and presumed ecologically similar forms (McGhee 1981). This constancy may lie behind the lack of common large-scale phyletic trends.

Stanley and Yang (1987) documented long-term stasis in 19 species of bivalve mollusks that persisted from Early Pliocene to Recent. When compared with geographic variation between pairs of selected Recent populations, change in 18 of the 19 lineages was insignificant. It is of interest that 7 of the lineages had previously been considered to be pairs of phyletic species. This suggests some question as to species identification, and one cannot be sure just how many biological species are represented in the study. Nevertheless, it is clear that no large-scale change has occurred. This may further strengthen the argument for stabilizing selection for overall form in benthic environments. Sheldon (1996) argued that shelf environments are quite variable, and this would select for generalized genotypes, capable of responding to a variable environment. One might also expect these genotypes to have a capacity for nongenetic plastic responses to different environments, whose temporal changes might be mistaken for evolutionary change.

Stanley and Yang (1987) found that intraspecific variation (differences between two contemporary populations) is of the same magnitude as differences among members of the same phyletic lineage. Both of these differences are significantly less than interspecific differences. This difference is interesting but not complete, as shown by a similar study of *Mulinia lateralis* (Brande 1979). A population of this bivalve reared in a predator-free cage was as different from typical *M. lateralis* as any other species! This difference was most likely nongenetic and demonstrates that ecologically extreme situations were overlooked in Stanley and Yang's study. In a sense, this only strengthens Stanley and Yang's case for stasis, as this makes the intraspecific contemporary variation potentially even larger than the extent of a long-term trend. It also suggests, however, that intra-versus interspecific comparison tests of variance are dubious without more geographically and ecologically diverse samples (as opposed to sample size in one area, which is very large in the Stanley and Yang study, and gives a false sense of security).

Long-term stasis prevailed in a series of gastropod lineages in the eastern Turkana Basin, but a "sudden" change in several lineages occurred within a 5,000- to 50,000-year interval (Williamson 1981). As discussed above, Williamson's study is liable to be stratigraphically complete, even at the resolution level of 1,000 years. The change was spectacular indeed, and radical morphological alterations were observed. According to Williamson, the strong and rapid changes occurred in an isolated lake within populations of large numbers. Stratigraphic evidence suggests that the changes occurred when the habitat was shrinking. There is some question as to the rapidity of change, because the major jump occurs at a formation boundary, which might include a gap (Boucot 1982). Even if the time scale is correct, as Jones (1981) noted, the period over which change occurs is relatively long for most population–genetic processes and therefore is hardly a challenge to neo-Darwinian theory. Furthermore, according to Williamson, it took place within an isolated basin with large population sizes. Thus, even though this basin was separated from others where no change occurred, it does not fit Mayr's requisites for a genetic revolution, as Williamson acknowledged. But it also does constitute phyletic evolution within one large population. One must even be somewhat suspicious that the change seen, in many of these Turkana gastropod groups simultaneously, including a parthenogenetic form, is perhaps an ecophenotypic response to strong changes in lake chemistry.

If Williamson's study actually recorded speciation events, it is likely that they resemble the many cases of ecologically driven speciation that have been observed especially in freshwater fishes, ranging from the spectacular divergences observed in cichlids of lakes in Africa and South America (Echelle and Kornfield 1984) to smaller flocks of just a few species, observed in temperate and boreal lakes (Riget, Nygaard, and Christensen 1986; Schluter 1996). Such changes are liable to be sudden and followed by stasis in the large lake regime. This may explain the conformance of speciation forces, which are driven by steep gradients that cause tradeoffs in performance in feeding and swimming behavior (Schluter 1996). It is possible that lake expansions stimulate environmental heterogeneity but also foster a relaxed selection regime that allows for greater phenotypic variation as a source of selection (McCune 1990). Early Jurassic lake fish faunas suggest that six species appeared in 5,000 to 8,000 years (McCune 1996).

One example of purported stasis in *Homo erectus* (Rightmire 1981) has some statistical problems likely to be present in other work. Owing to poor sample size and strong variability, the null hypothesis that stasis occurs cannot be falsified easily (Levinton 1982b, but see Charlesworth 1984a). Despite poor statistical analyses and small sample size, *Homo erectus* has been cited repeatedly as an example of stasis (Eldredge and Tattersall 1982; Gould and Eldredge 1977; Stanley 1979, 1981). An analysis by Wolpoff (1984) shows this to be incorrect. Nevertheless, near stasis has been found for size in the Eocene mammal *Hyopsodus* (West 1979), though large-scale (intergeneric) gradual change has been seen in the same geological sections for other taxa (Rose and Bown 1984).

The closer you look, the more gradual it gets? It should be no surprise by now that gradual transitions, not without reversals, can be detected best when sampling is detailed. Indeed, sparse sampling tends to lead to recognition of rectangular changes, because steady gradual change is unexpected, so we will perceive the sparse sampling as jumps (Sheldon 1996). So what happens when sampling levels are dense? Gradualism and evidence for transformations between anagenic strings of species, of course. Recently, Maureen O'Leary (in preparation) resampled the Wasatchian (latest Paleocene–Eocene) rocks of the Willwood Formation and produced the densest

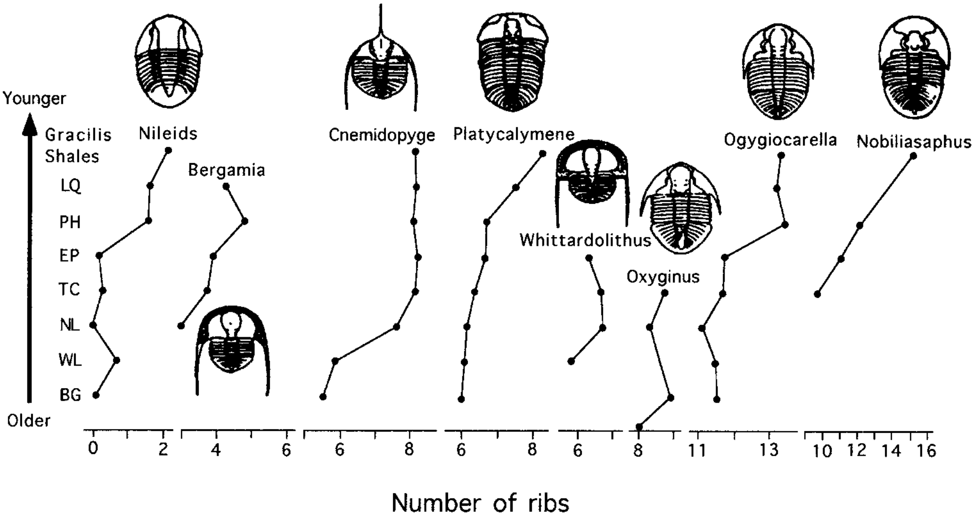

Figure 6.27. The wobble of evolution. Transitional change in eight lineages, including an intergeneric change in the family Nileidae. (After Sheldon 1987.)

sampling of mammal fossils over a long time period to date, with an average time between samples of about 160,000 years. Of course, that is still quite long by the standards of population biologists. In rocks representing a period of 2.9 million years, she documented the rise of several new species and one new genus, all arising by anagenetic change in a mosaic fashion of a number of characters, involving tooth shape and the development of an ectoconic notch on the lower molars (Figure 6.26). Although tooth characters change, an increase in body size suggests a transition from nocturnal to diurnal habits. Change between successive stratigraphic levels is too gradual to find obvious "species" boundaries. A similar story emerges from Peter Sheldon's documentation of trilobite evolution (1987) in the Ordovician at Builth Wells in central Wales. Here, the sampling density is excellent, coming in at an average of only 900 years between horizons. In this case, eight lineages of trilobites change transitionally up the section, so that identification of the anagenetic species transitions is arbitrary. Yes, there are reversals in the section, but that makes the change no less gradual (Figure 6.27). Of eight lineages, seven bridge the gap usually used to designate species-level differentiation, whereas one even bridges an intergeneric gap (Figure 6.28). As Sheldon (1996) noted, haphazard and sparse sampling leaves the impression of rectangular change, which fits with the "...descriptive biases, of what I term punctuational taxonomy..." (Sheldon 1996, p. 210).

The meaning of persistence of descendants with ancestors. When cladogenesis occurs, a descendant taxon may coexist with its progenitor. If speciation is allopatric, the new pair of species may have arisen from one formerly geographically continuous species, following the appearance of a geographic barrier (e.g., the Isthmus of Panamá). Alternatively, the progenitor species may have colonized a new region (range extension), and the colonizing population may diverge (e.g., colonization of deep water from

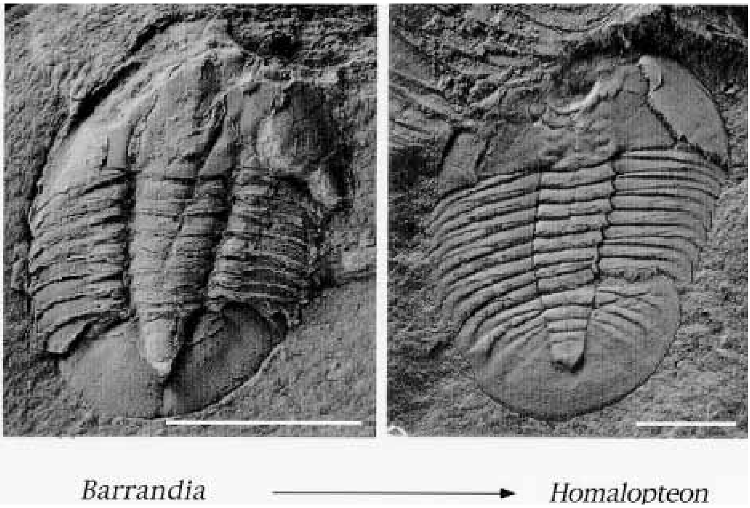

Figure 6.28. The nileid genera *Homalopteon,* which is ancestral in an anagenetic string leading to *Barrandia.* Scale = 1 centimeter. (Courtesy of Peter Sheldon.)

the continental shelf [Geary 1995]). Gould's ultimate (1982c) test of the punctuated equilibrium theory is the persistence of ancestral with derived species. Given the rigid requirement that the ancestral species was static, the divergence process is rapid, and that both descendant and coexisting ancestral species subsequently remain static, the punctuated equilibrium pattern is supposedly fulfilled (Figure 6.29, upper left).

Given that coexisting discrete morphs of a single fossil species can be easily misinterpreted as members of two genera, one can see that this test can be rather inefficiently put into practice. There is one important exception to this, however, and that is the case in which the taxa survive to the present, and some biological confirmation of species difference can be made. Alternatively, it would be useful to have a Recent standard of average species difference, against which differences among fossil taxa might be scaled. This approach, however, entertains the danger of ignoring the possibly many speciation events that may have occurred without any morphological change. It would be impossible in the fossil record to compare the number of biological speciation events with the degree of morphological change, if the former cannot be sampled adequately. Jackson and Cheetham (1990) demonstrated that the cheilostome bryozoan morphospecies, identified by allozyme differences, can also be discerned readily by morphological differences. The problem with their study is that the genetic differences between species are very large, even to the extent of completely different suites of alleles, which connotes great evolutionary distance (Avise 1994). The study simply does not rise to the level of precision needed for understanding the relationship of speciation and evolution. It is very doubtful that the species they identified readily are even sister species. If so, speciation is extremely rare.

The criterion of coexistence of descendant species with parent is as strong as our ability to identify species in the first place. The following four cases would all satisfy this criterion (Figure 6.29):

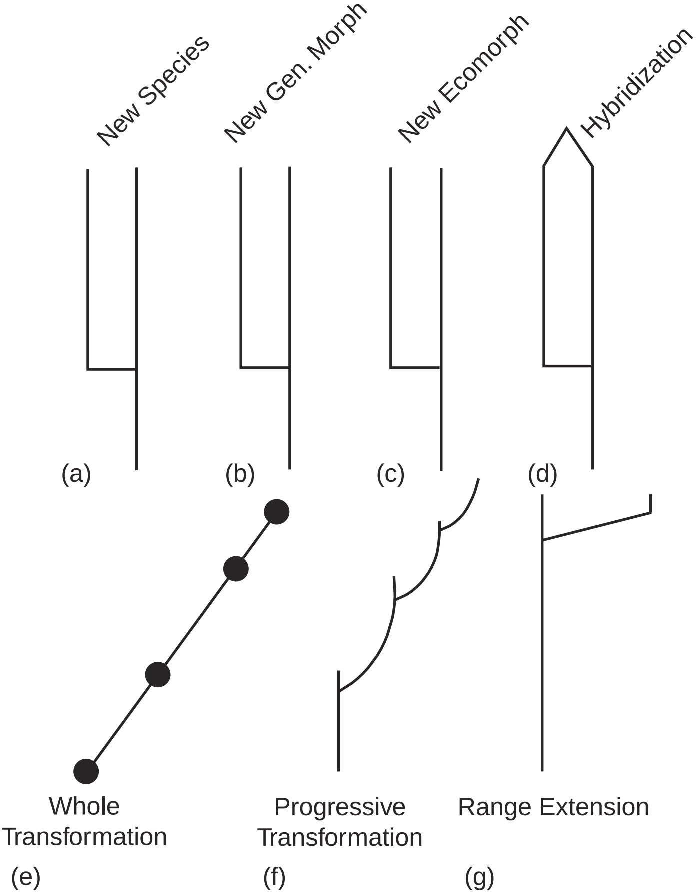

Figure 6.29. Top, four possible cases of taxa or morphs with static and overlapping temporal ranges: (**A**) punctuated equilibrium; (**B**) rise of new distinct genetic morph; (**C**) rise of new ecomorph; (**D**) hybridization. Bottom, models of regional transformation: (**E**) transformation of entire species in an anagenetic chain; (**F**) a continuous change in the environment favors a new form that evolves in one part of the range as a new species; eventually, the environmental change spreads, driving the progenitor species to extinction; (**G**) a range extension into a distinct environment.

1. A rapid speciation event generates a distinct daughter species, but the parent species survives unchanged. The daughter species does not change significantly during its subsequent history. Alternatively, one parental species divides into two (biogeographic questions of immigration must be understood) and both descendant species change at the time of splitting, but not subsequently.
2. Natural selection in a part of the species range rapidly generates a new and distinct morph, which comes to dominate local populations, or part of the species' range. The two morphs survive and persist unchanged.
3. Natural selection causes the evolution of a flexible but distinct phenotypically plastic response to environmental circumstances. Depending on local conditions, the population is dominated by one of several ecomorphs.

4. Divergence occurs by means of one of the first three mechanisms, but the distinct coexistence of divergent morphologies disappears, owing to hybridization (case 1) or a relaxation of selection (cases 2 and 3).

Cases 2 and 3 would pose significant difficulties for testing the persistence criterion, if distinct morphs could not be parsed from species differences. Distinct ecomorphs and genetic morphs are commonplace, particularly in groups in which simple mutations can produce large-scale morphological changes (e.g., Palmer 1985). The two alternative ecomorphs of the barnacle *Chthamalus anisopoma* demonstrate this well (Figure 6.8), as do other cases of phenotypically discrete plasticity. As fossils, populations dominated by these morphs would be regarded as mixtures of two distinct species. Even more notable is the rapid evolutionary response of two northern New England gastropod species to the arrival from Europe of the shore crab *Carcinus maenas*. Within a few decades, predation caused selection for distinct new morphs of the dog whelk *Nucella lapillus* and the periwinkle *Littorina obtusata*. In the latter case, distinct populations of thin-shelled, high-spired forms exist within a few kilometers of populations with thick-shelled, low-spired forms. This is strictly an intraspecific phenomenon (Seeley 1986), but it conforms precisely to the persistence criterion. The morphs are so distinct that they would almost certainly be classified as different species by paleontologists. Indeed, much more subtle differences may distinguish marine gastropod species. Worse than that, there is evidence to believe that the differences stem from phenotypic plasticity (Trussell 1996).

Very few conclusive cases fit the persistence criterion, but a study of Miocene–Pliocene bryozoa (Cheetham 1986; see also Cheetham and Jackson 1995) stands out for its excellent fit, with multiple branchings. Although the stratigraphic sampling is not very dense, there is no change within the history of “species” (these are of necessity defined strictly on the basis of morphology), which in the main give rise suddenly to distinct offshoots, the ancestors surviving and coexisting. On the one hand, the average stratigraphic resolution is 1.6×10^5 years. This certainly allows for extensive and plausible morphological change “between the cracks.” But, as Cheetham noted, the apparent lack of change through the rest of the history of most of the ancestral species does not admit to any phyletic evolutionary hypothesis. The approximate time of cladogenesis is the time of morphological bifurcation in most of the cases he studied. Unfortunately, the lack of knowledge of the genetic determination of the characters leaves this case moot with regard to issues of genetic revolutions, selection, and genetic drift. In addition, one cannot rule out the possibility that speciation is rampant, but morphological evolution occurs only occasionally when a population is forced into a marginal environment and subjected to rapid directional selection. What then becomes interesting is why the character complexes remain constant in the daughter species. This is, again, the issue of stasis, which I believe to be the legitimate problem spawned by the punctuated equilibrium model.

In the 1990s, a few new cases of persistence of daughter species have been documented, and these demonstrate the ambiguity of data when one attempts to pigeonhole cases as either phyletic gradualism or punctuation. Usually the real world is complex and filled with coexisting lineages that change gradually, remain the same, or often go off in reverse directions in similar morphological characters (Bralower and Parrow 1996; Sheldon 1987). Often a morphological character, be it mammal or foram, will continue to change gradually, irrespective of the production of new species (e.g., Mathers and Henneberg 1996, Norris et al. 1996). Open-ocean foraminifera show cases of splitting, but a thread of anagenetic ancestor–descendant species may still dominate. In a Miocene–Pliocene *Globoconella* anagenetic string of species, descendant species seem to extend the range of the clade into deeper water. Thus, there may have been coexistence of species that arose through cladogenesis, but the depth effect overall creates a classic morphocline that is determined by natural selection and may not even have involved speciation (Schneider and Kennett 1996).

When splitting occurs, it may be that the daughter species is an invader of a new habitat. But if the environment is shifting, then the ancestral species might hang on for a while but then might become extinct, as it cannot track the environmental change. This pattern would be accentuated if the "new" environment first appeared in part of the ancestral species' range. Then the daughter species would simply be a geographically restricted subset of the ancestral species that buds off. As the new environment swamps the entire ancestral species' range, it might be driven to extinction. A simple example of such a change would be a general cooling, which began at high altitudes and spread to valleys. This selection-speciation scenario is effectively one of directional selection: The descendant species adapts to the change and displaces the old species as the new environment spreads. For a brief period, however, the ancestral and descendant species might coexist in time, if not in space (or microhabitat). Pearson (1998) analyzed a number of cases in nannofossils, graptoloids, and planktonic foraminifera where an ancestral species budded off a descendant species. The descendant species was significantly more likely to survive relative to the ancestral species, supporting the idea of adaptation, which led to progressive speciation. This result is inconsistent with the punctuated equilibrium prediction of random directionality in speciation.

Jackson and Cheetham (1999) argue that 29 out of 31 cases of speciation culled from the literature fit the punctuated equilibrium argument but failed to mention that 22 of these cases come from their own work within just two clades of bryozoa. The *Prunum* case is ambiguous at best, as discussed above (in section called Can Fossil Species Be Identified?). Lastly, they cited 6 species of the Miocene gastropod *Melanopsis* (Geary 1995), but this, too, is misleading. From Geary's qualitative account it certainly appears that an apparently monophyletic clade of 6 species appears suddenly, but whether there is subsequent long-term stasis is not even documented. Moreover, this clade has a sister clade that *is* dominated by gradual evolution. Admittedly the sister clade has only two species, but any notion of statistical independence would require placing this clade on equal statistical footing with the "sudden-speciation" conclusion for the other clade. The problem with Jackson and Cheetham's interpretation is the false dichotomy, which leads more usually to rhetoric than substance. Geary (1990, 1995) did not fall into this trap, having noted that melanopsids show a "range of evolutionary tempos."

I contend that a more expansive understanding of the context of allopatric speciation suggests that the persistence criterion is far more ambiguous and renders punctuated equilibrium just an undeservedly highlighted instance of neo-Darwinian processes. Consider the case in which the environment shifts in the same direction and gradually throughout the whole geographic region. If there is a morphological response, we would expect in the fossil record to see a temporal anagenic chain of transitional "species," recognized by arbitrary thresholds of morphological difference (Figure 6.29E). The most extreme linear version of this, of course, is the so-called model of gradualism, demonized by Eldredge and Gould (1972). But geographic factors immediately make this model far too simple. Consider the case in which the environment is changing steadily but important evolutionary changes appear first in one part of a species range. A simple example of this would be a global cooling that first affects a species at high latitudes. A new distinct taxon would appear (Figure 6.29F) and would coexist temporally with its ancestor. But as the environment cools everywhere, the descendant would take over and the ancestral species would become extinct. According to Pearson (1998), the preponderance of fossil temporal chains of species fits this model best, suggesting that speciation is merely driven by adaptation, with a time lag that is driven by gradual spread of a new species over areas corresponding to a new environment. In a way, this is a punctuational process, but it is driven entirely by patterns of natural selection, modulated by geographic substructuring.

A simple range extension (Figure 6.29G) might also fit the punctuational pattern. But this is not very surprising, given the potential for extremely rapid evolution when a population invades a new habitat (Huey, Gilchrist, Carlson, Berrigan, and Serra 2000; Klerks and Levinton 1989), sometimes even leading to assortative mating of individuals adapted to a new subhabitat (Rundle, Nagel, Boughman, and Schluter 2000).

I am impressed with how little in the way of evidence supporting the dominance of punctuated equilibrium has been found, despite over 20 years of searching. Stasis is still used as evidence, when nothing much more is known (Gould and Eldredge 1977; Jackson and Cheetham 1999). But stasis is not good enough, even if it is an interesting phenomenon. Yes, Cheetham and Jackson's study of bryozoans is exemplary. Moreover, I can point to a very nice study of Quaternary short-tailed shrews (genus *Blarina*) where two species' distinctive morphology must have appeared at or about the time of splitting, with subsequent stasis (Jones, Choate, and Genoways 1984). The morphological change, however, was driven by a subdivision of the environment, so regional diversifying selection was the cause. Most other examples are like this and leave one with a sense of ambivalence or, worse, irrelevance.

The blesbok-hartebeest-wildebeest group has high extinction and speciation rates, with trends toward complex horn shapes. These result from specialist grazing, but the individuality of horn configurations must be strongly influenced by sexual selection. In contrast, impalas show generalist grazing, with little speciation, despite low gene flow and clumped distributions (Vrba 1980). What are we to make of this? Not much, I would contend. Of course, a species recognition trait is by definition a potential element of the speciation process. But sexual selection can readily occur also as an anagenetic process, accelerated by a runaway process that may actually run fitness down (Kirkpatrick 1982, 1987; Lande 1981), or it may occur by selection for fitness-associated signals (e.g., Alatalo, Hîgland, and Lundberg 1988). Some sexually selected traits may be under strong stabilizing selection, owing to a balance between ornamental and armament functions (Berglund, Bisazza, and Pilastro 1996). Vrba (1983) pointed out that anagenetic trends are possible and are compatible with – not anthithetical to – additional speciation-associated morphological change.

As mentioned in chapter 3, some evidence exists bearing on the issue of genetic variation, morphological variation, and speciation rate. There is too little to really tell at present, except for the mammals. Carroll (1997, pp. 108–109) made a compelling case against a role for speciation in morphological divergence in Pleistocene mammals. Speciation rate in mammals is a strong function of body size, which, in turn, is probably inversely related to the degree of isolation among subpopulations, which enhances speciation. Thus, genera of small body size have far more species than those of large body size. If speciation rate were a driving force in evolution, one might expect morphological evolution to be more prominent in small forms, but the reverse is so. Kurtén (1968) described 43 instances of species-level transformations in European Pleistocene mammals, but 20 of these involve large-bodied forms and only 8 comprise small-bodied species, the rest being intermediate in size. Failing this test, it becomes clear that the importance of any hierarchical processes, such as the potential for sorting among species, is diminished entirely.

If there is a bottom line, it is this: Our current estimates suggest that the slow rates of evolution estimated from broad temporal scopes are an illusion; evolution is much faster when estimated from shorter time periods, perhaps even as fast as natural selection in a population cage. But if rates are fast on the short run, it is absurd to think of sustained directional change in most cases; this would lead to absurd morphologies and body sizes. Thus, fluctuation of direction is common, but transitions between morphologies of species and even genus-level difference are also quite common. The large number of examples we have of transitional change and anagenetic species strings are the proof of the pudding of transitional hypotheses. The lack of consistent association of speciation rate with morphological change in living forms and the lack of even a modest number of fossil cases accentuate the failure of punctuated equilibrium.

Phyletic Gradualism: The Making of a Straw Man

Who really was a pure gradualist? The proponents of punctuated equilibrium successfully installed a new slogan by inaccurately characterizing Darwin's original work, the attitudes of some paleontologists, and the body of work produced by evolutionary biologists in the first half of the twentieth century. It is a measure of their success that many of the architects of the Modern Synthesis and their disciples have been forced into the situation of defending a position in which they had never believed. It's much like asking the question *Have you stopped beating your wife?*

The straw man of phyletic gradualism was built up in two stages. First, Darwin's conception of evolution was represented as a belief in the slow and even transformation of entire species into new morphological entities. Stanley's (1981) *New*

Evolutionary Timetable envisioned Darwin as frozen into the position that even gradual change was the only sort possible:

> Even if Darwin had possessed theoretical reasons for adopting a punctuational model of evolution, for him to have advanced such a scheme would have seemed as absurd as were many of the speculative pronouncements of his predecessors. [He] would have been claiming that evolution … was operated by a natural mechanism … in small, localized, transitory populations. [quote from Stanley 1981, assembled by Rhodes 1983]
>
> It was a measure of Darwin's desire to underscore slow, continuous modification that he violated his own philosophy of empiricism and reached back into history for what is essentially religious dogma. [Stanley 1981, p. 47]

Many have discussed the inaccuracy of this general claim (Levinton 1982c; Penny 1983; Rhodes 1983). Darwin certainly believed that evolution often occurred in isolates. Indeed, this was one of his two major explanations of sudden change in the fossil record. As Darwin argued:

> Varieties are often at first local … rendering the discovery of intermediate links less likely. Local varieties will not spread into other and distant regions until they are considerably modified and improved; and when they do spread, if discovered in a geological formation, they will appear as if suddenly created there, and will simply be classed as new species. [1859, p. 464]

Darwin would have fit well in Eldredge's (1971) article on rectilinear evolution in the trilobite *Phacops rana*. It is also the common argument (see, e.g., Jeletzky 1965) given by paleontologists for sudden change in the fossil record at low taxonomic levels.

Darwin believed similarly, at least by the sixth edition of *The Origin,* that most species-level differentiation occurred in periods very short relative to the entire history of the species (Penny 1983):

> …it is probably that the periods, during which each underwent modification, though many and long as measured by years, have been short in comparison with the periods during which each remained in an unchanged condition.

So I ask, yet again: What is all the fuss about? Darwin's views are compatible with at least three of Eldredge and Gould's (1972) criteria characterizing the empirical pattern implied by punctuated equilibrium: (1) new species develop rapidly and morphological change is rapid relative to the entire history of the species, (2) the change is concentrated in a geographically restricted population (although Eldredge and Gould, following Mayr's [1963] lead, would have the population be at the periphery of the species' range), and (3) the change occurs in a small subset of the entire ancestral species.

Even the first edition of *The Origin* did not accept the "purest form of Darwinian gradualism" ascribed to it, as mistakenly claimed by Gould (1980b, p. 122). In discussing his famous and hypothetical diagrammatic example of a phylogeny, Darwin rejected even rates of evolution by stating that he did *not* suppose that evolution goes on so regularly as expressed in the diagram. There is no evidence, despite the claims of Gould and Eldredge, that Darwin ever believed in absolutely constant rates of evolution. From the beginning, *The Origin* acknowledges the geographical complexities of evolution. It's easy to ask: What is the fuss about?

The same degree of exaggeration is apparent in the punctuativists' characterization of the Modern Synthesis. As Levinton and Simon (1980) discussed, the Modern Synthesis is hardly a unified claim for gradual evolution at homogeneous rates. Speciation is a polyglot process, incorporating everything from accumulation of isolating genes to strong selection for prezygotic isolation (see chapter 3). Many believe that genetic reorganization during speciation either is predominant (e.g., Mayr 1963, 1982b; White 1982) or at least occurs commonly (Templeton 1981). The work of population geneticists and other evolutionary biologists in no way conforms to the gradualist picture presented by Eldredge and Gould. Haldane (1932a) recognized that speciation was often sudden and noted (p. 59) that species "can arise at one leap."

Stanley (1979, p. 72) impugned the Modern Synthesis for relying on phyletic evolution, a supposedly slow process, to generate the bewildering amount of morphological diversity in evolution. On the broad scale, many paleontologists and neontologists have been impressed with the slow rates of change in fossil lineages. As noted above, Haldane (1949) was deeply impressed with the apparent slowness of morphological evolution. But this questioning of evolutionary rates is hardly unique either to punctuativists or to Haldane. Indeed, Simpson (1953) mentioned this very troubling issue:

> The morphological difference between modern opossums and some Cretaceous opossums is slight, but some 60 million years of evolution occurred between them. If the missing pre-Cretaceous sequence changed at a comparable rate, the transition from a reptile to an opossum can hardly have taken less than 600 million years; it probably took several times that long – in short it must have occurred in the Precambrian, which is certainly absurd. [p. 351]

Simpson concluded that rates of phyletic evolution varied tremendously (from quantum evolution to slower rates). Stanley differed in believing that some special feature of speciation was necessary to accelerate evolution, but certainly the problem of variable evolutionary rate has long been appreciated. Again, what is the fuss about?

In concocting their straw man of phyletic gradualism, Eldredge and Gould (1972) characterize the tone of textbook representations of paleontological thought by selective quotation. After misquoting Darwin as seeing speciation as (p. 89) "a long and insensibly graded chain of intermediate forms," they argued that "our present texts have not abandoned this view." But what do the texts actually say? Moore, Lalicker, and Fischer (1952), authors of one of the two preeminent texts of the 1950s and 1960s (the time in which Eldredge and Gould were educated in paleontology), presented the two alternative models of transformation within lineages and splitting (i.e., speciation). But what did these authors say about the tempo of change in fossil lineages? On page 35, they suggested the following:

> The fossil record indicates that evolutionary rates are by no means uniform either in different stocks or in the same stock in different times. Some organisms exhibit such extremely sluggish evolutionary modification that they seem to stand still, whereas others undergo amazing sorts of morphological change with geological abruptness. Also, paleontological study of various lineages indicates that periods of slow, gradual adap-

> tive change alternate with "explosive" spurts of evolution. These accelerated bursts develop descendants which differ markedly from their ancestors in form and function. The lack of known fossil connecting links between various orders and classes of the animal kingdom suggests that their origin may lie in this type of accelerated evolution or abrupt divergence.

Eldredge and Gould reproduced Moore et al.'s figures, but how they missed this clear statement is anyone's guess. The same can be said of the other important text of the period, Easton's (1960) *Invertebrate Paleontology*. It is true that Easton expounded on the utility of evolutionary series and claimed that there are transitional forms. Guess what? He was right about that! But he illustrated only one example of species-genus-level evolution in his entire text, the evolution of a Cretaceous cheilostome bryozoan group. This study showed both cladogenesis and transformational series of "species." The phyletic chains of species showed parallel evolution. Again, the real world of fossils, as seen by paleontologists, doesn't quite fit the gradualist demonology erected by Eldredge and Gould. So, yet again, I ask: What is the fuss?

Paleontological practice: Species stasis enmeshed in broader trends. Is there a reason why phyletic gradualism would be thought by punctuativists to be such an important ideological target, beyond the apparent error of attributing its credo to either Darwin or the Modern Synthesis? Indeed, have paleontologists been deceived by the phyletic gradualist "dogma" and thus been affected in their respective researches? This question is approached by Penny (1983), who noted that "phyletic gradualism as defined by Eldredge and Gould … appears more consistent with orthogenesis than with Darwinism" (p. 73). Phyletic gradualism, as described by Eldredge and Gould, comes from the old paleontological and morphological traditions begun in the early and mid-nineteenth century. These traditions searched for gradual change at levels of resolution of tens of millions of years, and *not* within the range of a single species. The claim of a belief in gradualism by paleontologists is bogus and misleading.

The punctuation–gradualism dichotomy seems peculiar when it is juxtaposed with paleontological practice at the species level. Paleontological species are erected in the hope of dating rocks with biostratigraphic correlations. Most studies of invertebrate microfossils and macrofossils yield sequences of fossil "species" whose recognition is based on a threshold of perceived phenetic distance (Kaufmann 1933; Levinton and Simon 1980; Newell 1947; Sheldon 1993). Such practice tends to select for the definition of paleontological species as entities with implied geographic homogeneity and temporal constancy. Cases in which the gradual evolution of characters was used to accomplish biostratigraphic correlations (e.g., Smith 1945) are rare relative to species zone correlations. Stratigraphers may have believed that there were intermediate forms, but this rarely entered into their actual practice, which focused on any characters defining some or another discontinuity.

Punctuation, therefore, *is* the typical paleontologist's intuitive bias in biostratigraphic practice. The underlying objective – to give species zone names to time horizons – directs paleontologists to search for static taxa, or at least to pretend that they are static. Cisne et al. (1980) documented how this sort of bias led a paleontologist to identify two distinct "species" of the trilobite genus *Triarthrus* with supposed stratigraphic significance, but the two forms were end members of a continuum of variation. Sheldon (1987) found this same result for many lineages of Ordovician trilobites in Wales. Major sedimentary breaks may be used as convenient breaks for species delineation (e.g., Stenzel 1949), but paleontologists never saw these as anything more than opportunities to identify biostratigraphic zones.

The prejudice in favor of punctuational-type species sequences in constructing biostratigraphic zones is well stated by the invertebrate biostratigrapher Jeletzky (1955, p. 485):

> Equating all kinds of evolutionary changes observed, such authors tend to express in terms of conventional taxonomic units and to name as species individuals possessing even the finest morphological distinctions without due regard to their intergradation or the stability of their morphological distinctions in time and space. This attitude may also well be caused by the widespread but unfortunate feeling that a species is an essentially *morphological, static and at the same time smallest recognizable category.* [Italics mine]

As Jeletzky so aptly recognized, paleontologists were punctuational in approach. Neither Darwin nor the Modern Synthesis did much to change the paleontological practice of "variety hunting."

On the one hand, paleontologists see the problems of species recognition between major paleogeographical realms and over time (e.g., Imbrie 1957; Newell 1947; Shaw 1969). They must name species, on the other hand, according to the rules of the International Commission on Zoological Nomenclature. The resulting frustration is illustrated by Shaw's 1968 Paleontological Society presidential address: "I have come to the conclusion that the concept of species is misleading, inappropriate, and useless in professional paleontology" (Shaw 1969, p. 1085).

Paleontological research rarely was done at the level or with the stated intent discussed by Eldredge and Gould. This is why the historical argument of the belief in phyletic gradualism at the species level is so misplaced. Gould and Eldredge (1977), for example, ridiculed one of paleontology's favorite examples of gradualism, the evolution of *Micraster,* because it consists of just three successional species from few horizons, sometimes having reversals in character trends from species 1→2→3. But Rowe's classic study (1899), as much as it is cited in some paleontology textbooks as a case of evolutionary transition (e.g., Raup and Stanley 1971), was *not* intended to demonstrate gradual evolution. It was designed instead to demonstrate that unique morphologies could be used to delineate stratigraphic horizons (see Rudwick 1972). This study was an attempt to distill singular entities, corresponding to species names, from a wealth of usually gradational variation. Consider Rowe's (1899) remarks:

> We must either make a species out of every trivial variation, or mass certainly obviously allied forms into groups. . . . It is only by this means that passage-forms [transitional forms between defined species] and mutations can be intelligibly arranged. [p. 541]
>
> In reviewing this Protean genus . . . it would be easy to place a series on a long table, and to show an almost imperceptible transition from one form to another, and yet from that same series to pick out specimens which would serve as museum-types of the several well-known species. [p. 497]

This is not to say that Rowe did not claim modes among the types. He acknowledged a great deal of morphological variation, yet still chose to name successional species in a summary table, probably characterized by arbitrary differences. Rowe's judgment of gradational differences between "species" was confirmed in later studies (Kermack 1954; Nichols 1959). Rowe also recognized transitional change within one species, an observation omitted by Gould and Eldredge (1977).

The typical skeptical attitude of paleontologists toward the species level usually shifted emphasis away from small-scale studies of morphological change in a stratigraphical column. Paleontologists believed that the species in paleontology was essentially an unworkable level of paleontological research; hence Simpson's (1944) proper claim of ignorance of paleontological evidence at this level of resolution. It is a telling point that the famous *Genetics, Paleontology, and Evolution* (Jepsen, Mayr, and Simpson 1949) was conspicuously lacking in studies attempting to show small-scale change in the fossil record. Indeed, few such careful sampling studies had ever been performed. Brinkmann's (1929) classic study of the ammonite *Kosmoceras* is a glaring exception. Cloud's (1948) seminal article on evolutionary trends, discernible from paleontological data, dealt only with trends on the scale of millions to tens of millions of years. Rudwick (1972) has argued that Darwin's emphasis on the supposed incompleteness of the fossil record may have discouraged paleontologists to collect fossils in closely spaced stratigraphic intervals to document transitional evolution. On the other hand, Allen (1979) argued that midnineteenth-century paleontologists and geologists, in developing their new profession, used an inductive approach not conducive to the interdisciplinary approach required to link with Darwinism. In any event, paleontologists were not thinking at the small-scale level of species. As Weller (1960, p. 556) remarked in his classic text on biostratigraphy: "species have been little employed in attempts at evolutionary reconstruction ... phylogenies generally are based on the presumed relations of genera."

Although Eldredge and Gould were incorrect in claiming that paleontologists have been assuming and searching for phyletic gradualism at and below the species level, their argument does reveal the confusion between the timescales considered by paleontologists and those examined by neontologists. It was no accident that the 1980 meeting on macroevolution, at the Field Museum in Chicago (Levinton and Futuyma 1982), was held at a time when population geneticists were surprised at what was to be considered by paleontologists a "short" time interval for evolutionary change at the species level; tens of thousands to hundreds of thousands of years was a typical answer. For workers accustomed to a literature registering speciation events within hundreds to a few thousands of years, and considerable morphological change in field populations within decades to years, this was a bit of a shock. Paleontologists took a neontologist's eternity to be a "geological microsecond."

Consider Henry Fairfield Osborn's (1934) approach to the evolutionary paleontology of the Proboscidea. Taking grand sweeps of lineages from the Eocene to the Pleistocene, a period of 40 million years, he nevertheless felt able to criticize Bateson's mutation theory and suggested his own theory of the nature of variation and differences among evolutionary novelties. Even though his minimum time resolution was usually several million years, he was able to assert confidently in the picturesque language no longer found in the current pages of the *American Naturalist*:

> ...the first grand result is the replacement of all ... hypotheses of "discontinuity" and of breaks between species. These time honored difficulties melt away like a block of ice in the glowing sun of observation of the actual modes of phylogenetic origin of adaptations. [1934, p. 213]

Osborn's scale of time resolution could never have resolved the short-term dynamics of the evolutionary process. His study, nevertheless, sketched a wonderful picture (Figure 6.30) of gradual change.

Eldredge and Gould's (1972) phyletic gradualism is not a belief held by neontologists or Darwin or even a formula for a research program practiced extensively by paleontologists working at or below the species level. Eldredge and Gould, both educated as paleontologists, were trained to believe that large-scale trends were the stuff of evolutionary study. (Gould [1980a] acknowledged Simpson [1953] as his textbook source when he learned evolution.) It was only natural to misinterpret these trends as being microevolutionary, not because paleontologists ever investigated evolutionary change at small scales, but because they maintained a fuzzy connection between grand evolutionary trends and short-term concepts used by neontologists such as natural selection. Although I disagree with Eldredge and Cracraft's (1980) characterization of Simpson's confusion with the connection, I do

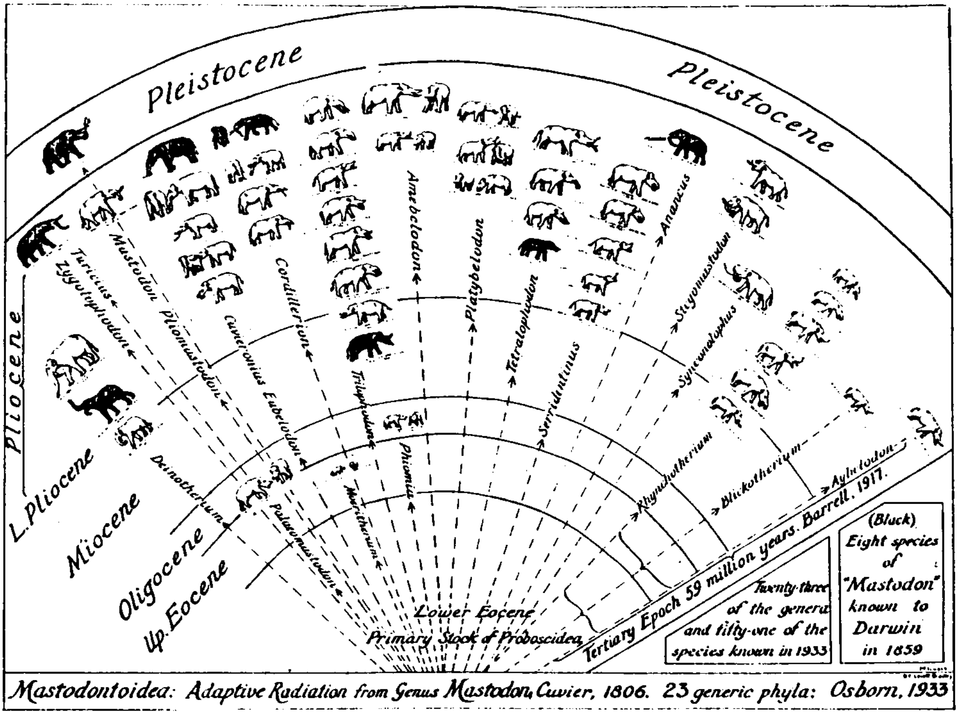

Figure 6.30. H. F. Osborn's conception of evolution in the mastodons. (From Osborn 1934, with permission.)

think that they exposed most paleontologists and neontologists in a common confusion among timescales and evolutionary events.

Taxonomic longevity and evolutionary rate. Cherry, Case, and Wilson (1978) discovered a remarkable relationship between genetic relationship and taxonomic level in frogs. It was possible to obtain a linear relationship between genetic distance, based on microcomplement fixation, and ascending taxonomic rank, suggesting that there is a correspondence between genic and morphological differences. But these workers showed that such a comparison cannot be extended from one group to another. The degree of morphological difference between humans and chimps is much greater than among frogs, when scaled against the degree of biochemical differentiation. Intergroup comparisons of morphological differentiation are therefore poorly indicative of genic difference; relationships found within members of a clade may be the result of group-specific genetic characteristics, perhaps in gene regulation.

Paleontologists commonly assume that equivalent taxonomic levels in distantly related groups can be employed profitably to contrast rates of morphological or genomic evolution. Simpson (1944) constructed frequency distributions for molluscan and mammalian families and found that mammal families were of far shorter duration. From this he concluded that mollusks evolved more slowly. Stanley (1973a) did a more detailed analysis using bivalve mollusks and came to the same conclusion. He asserted that it was likely that mammalian evolution was accelerated by interspecific interactions, which were presumably less intense among marine bivalves. Stanley (1973a) found that the rate of first appearances of Cenozoic mammal families decreased steadily toward the present, whereas bivalve families instead showed an increase in rate of appearance from the Ordovician to the Neogene. To Stanley (1973a, p. 492) this was evidence that there was an "absence of restraints on diversification."

As we shall mention further in chapter 7, decoupling of taxon richness between different taxonomic levels is common and rather unpredictable. Until the Jurassic, there is a close correlation between appearance rate at the family and superfamily levels (Figure 6.31), but the post-Triassic shows a significant difference; the rate of appearance of families continues to increase in the Cretaceous and Tertiary, whereas the rate of superfamily appearance declines, much like the pattern for mammalian families. Overall, there appear to be two stages of decline, a Paleozoic stage followed by a post-Triassic decline. These results call into question the assumption that two taxa as different as mammals and bivalves can be blithely compared as if there was some absolute meaning to the taxonomic level of family. In this case, which taxonomic level of bivalves is equivalent to mammalian families: family or superfamily?

Can we relate morphological evolution to taxon longevity? Within a taxon, this seems to be a reasonable assertion, as in the case mentioned above for frogs. But it is not clear that one can relate groups as different as mammals and mollusks on the same taxonomic scale. Speciation events may not be as detectable in morphologically simple groups, such as protobranch bivalve mollusks, whose shells are relatively simple and often devoid of sculptural detail. A study by Schopf et al. (1975) further suggests the futility of intergroup comparisons of taxon longevity. A positive correlation was found between extinction rate and the number of morphological

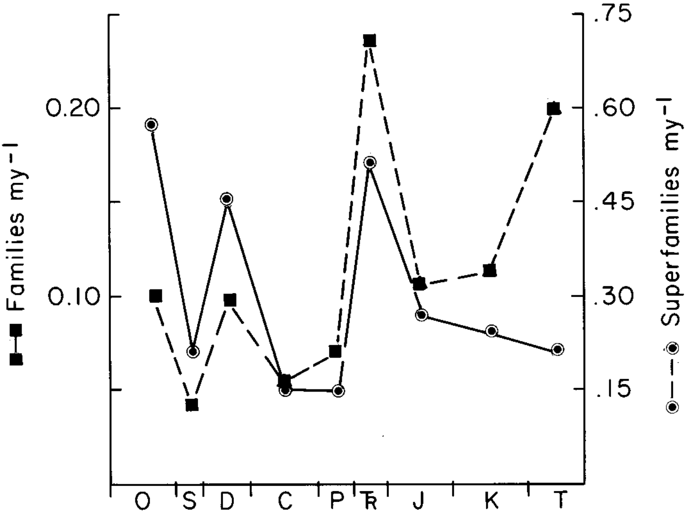

Figure 6.31. Rates of appearance of families and superfamilies of Bivalvia. (Data from the *Treatise on Invertebrate Paleontology.*)

terms used to describe the morphology of a taxon. The data fell into three groups; most notable are the mammals and ammonoids, with the highest number of terms and extinction rates. At the least, this result suggests a degree of difficulty in making intergroup comparisons, as it calls into question the possibility of using uniform criteria to establish common taxonomic levels across a group of taxa of strongly varying morphological complexity.

The correlation of genetic differentiation with morphological diversity shown above for frogs might suggest that it is possible to extrapolate rates of evolution to the degree of taxonomic longevity. If we have a phyletic series of "species" and there is some uniform notion of the degree of morphological differentiation associated with species differences, then species longevity should be associated with the rate of morphological evolution. Unfortunately, there are no careful studies to determine whether criteria for phyletic species recognition are at all uniform during the history of a clade. A good example of the possible problems that might arise comes from a summary of mammalian species longevity through the Cenozoic (Kurtén 1959b). Paleocene and Pleistocene species longevities were both significantly less (by a factor of approximately 5) than in Neogene mammals. Of special interest is the Pleistocene mean value of only 0.62 million years, the minimum longevity recorded by Kurtén. If longevity, and by extension, speciation rate, are accurate measures of evolutionary rate, then one must ask why it was so low in the midst of the major Paleocene radiation of mammals and equally low in the Pleistocene when no new major groups appeared. In the former case, brief longevity may indeed be correlated with rapid morphological evolutionary rate. But in the latter case, sudden extinction or perhaps evolutionary response to changing climate might have contributed to reduced longevity

In summary, taxon longevity or rates of appearances at the same taxonomic level should not be used for comparisons among taxa of great biological difference. Unfortunately, we have no database to know how different taxa can be before such comparisons are invalid. The morphological and genetic differences appear to be scaled totally differently among phyla. Moreover, it may also be invalid to use taxonomic longevity even within a single major group at different times during its history. Criteria for taxon recognition may change substantially. Comparisons should be restricted to closely related groups in which the morphological criteria for fossil recognition at a given taxonomic level are known to be homogeneous.

The Assembly of a Complex Bauplan

The major phyla, and sometimes different taxonomic classes or orders, are often thought of as a series of baupläne, with no intermediates. The concept of bauplan springs from idealistic morphology and therefore has a typological connotation. We all seem to recognize, nevertheless, a series of distinct body plans at the phylum and class levels, and the term can still be used to designate these groups. The presence of baupläne raises two important issues: (1) Is the very organization of a bauplan a source of evolutionary inertia? In chapter 4, we defined the possible sources of this inertia, in developmental, genetic, and adaptational terms. (2) Are the gaps among baupläne achieved in single crucial (and nonadaptive) leaps or is the process gradual and cumulative?

It may be sufficient to document change through a geological section to justify the phyletic nature of single-character evolution, but an attribute such as "mammalness" cannot be restricted to one character, even if the definition of the group can be made in this way (Crompton and Jenkins 1973; Simpson 1960). The success and ecological position of mammals owes as much to homeothermy, reproduction, and a complex central nervous system as it does to the acquisition of a new jaw joint and more complex teeth. This is, after all, the crux of any macroevolutionary question:

1. What is the pattern of acquisition of the many features?
2. What controls the pattern and rate of acquisition?
3. Once acquired, what holds the plexus together, if anything?

These macroevolutionary questions can be treated independently of the issue of speciation. The pattern of acquisition of various mammalian traits can be entirely coincident with speciation events or may consist of entirely within-species phyletic evolution. But as long as the mammals, with all of their unique characters fully formed, did not arise in a single speciation event, the questions still have relevance.

Three end member patterns can be imagined for the acquisition of the characters making up a complex group:

1. *Saltational hypothesis:* First, all characters could have been acquired at once. I don't believe that anyone takes Schindewolf's (1936) claim that the first bird hatched from a reptile's egg very seriously, without accepting some clever definitions of bird and reptile. Gould (1980a) revived the notion of hopeful monster, but certainly not at the level of wholly new organized body plans. Gould (1984a, pp. 185–186) argued, nevertheless, for the "enormous reservoir of potential for rapid evolutionary change" in developmentally significant mutations.

2. *Independent blocks hypothesis:* The features that characterize groups such as the mammals might be ascribed to distinct blocks, and these blocks might have evolved independently. As time progressed, interactions between the blocks occurred but only because of coincidental response to the same new environment, although later functional interdependencies among the blocks may have arisen. This has also been termed *mosaic evolution* (see de Beer 1958).
3. *Correlated progression hypothesis:* Different morphological complexes can be distinguished, but they have a sufficient interrelationship such that each system appears to "evolve in a loose correlation with all the other systems" (Kemp 1982, p. 313), maintained by function.

I support Kemp's (1982) hypothesis that correlated progression is a major component of mammalian evolution. Over time, the system has congealed from both a functional and developmental point of view, to the point that evolution to maintain the whole is probably as important as evolution designed to adapt independently any particular block to a change in the environment. I emphatically do not imply that this will be the case for all groups. Indeed, because theory does not predict unique solutions in most cases, our approach to such questions must be largely inductive. Mosaic evolution is a major component of the rise of baupläne, and, in some cases, single key innovations may have set the stage for the evolution of a large suite of associated features. For example, the molluscan bauplan may have derived from the acquisition of a hard dorsal integument, by a flatwormlike ancestor.

The evolution leading to mammals is unique in that a remarkable gap in morphological organization seen in living forms between mammals and reptiles is bridged in the fossil record with an array of intermediates (Crompton and Jenkins 1968, 1973, 1979; Kemp 1982; Parrington 1971). This is particularly interesting, given the considerable evidence that additional discoveries are likely to be made with increased sampling (e.g., Jenkins, Crompton, and Downs 1983). As it now stands, the fossil record of the mammallike reptiles (synapsids) documents approximately 130 million years of change from their earliest appearance in the early Upper Carboniferous to the first appearance of the "true" mammals in the Upper Triassic. Because the continents were not separated during this period, faunas were geographically relatively homogeneous, and incomplete sections in one location can therefore be filled in, at least at a coarse scale, with collections from other localities. The earliest mammals, found in Wales and northeastern Arizona, already show a diversity of jaw structure (Jenkins et al. 1983), so we are far from knowing the complete story.

The synapsids made their first appearance in the Late Carboniferous. They dominated the reptilian faunas until the end of the Triassic but then declined, to be followed by dinosaur dominance in a second age of reptiles in the Jurassic–Cretaceous. During this period, their descendants, the mammals, played a minor role in terrestrial faunas and were typically diminutive in size. The shift from dominance by obvious reptilians such as the pelycosaurs in the Permian to groups much more mammalian in character in the Triassic is believed to be associated with a general adaptation to terrestrial life (Kemp 1982). This would imply that the groups extant in the Triassic were superior to their predecessors at surviving the exigencies of terrestrial life. We must remember, however, that this superiority did not guarantee a place of dominance in the terrestrial world. Indeed, the dinosaurs seem to have forestalled the rise of the mammals for a considerable period of time. Trends seen within a group do not imply superiority to anything other than their own antecedents. It is unfortunate to think of the mammals as superior to the dinosaurs, or, for that matter, to think of the dinosaurs as inherently superior to the mammallike reptiles.

The distinction between advancement within a clade and interclade superiority is crucial. The former can be argued on functional morphological grounds, whereas the latter can only be argued from historical evidence of interclade competition, which is often weak or nonexistent (Benton 1983a, 1983b). Even within the synapsid clade, "advancement" can be considered only within the context of the characters that are associated with terrestriality per se. Many unique features acquired by members of the clade may have momentarily been more important in survival than the features associated with the overall trend toward "mammalness."

Many characters that we associate with "mammalness" – heart and double circulation, sweat glands, hair, lactation and parental care, an impermeable skin, production of a hypertonic urine, and a larger number of mitochondria per cell – cannot be documented meaningfully at this time from the fossil record. We are thus left with those characteristics that can be inferred directly and indirectly from the cranial and postcranial skeleton. We paint a picture with a palette of few colors. Skeletal characters can reveal much about physiology and activity, but not everything. We have, for example, a very incomplete picture of temperature control. Even among the extant homeothermic mammals, large differences exist in the absolute value of temperature, even if the temperature is maintained relatively constant. In fossils, there is a strong case for homeothermy in derived mammal-like reptiles and dinosaurs, based on the lack of seasonal growth rings in bones, other features of bone structure, and predator-to-prey ratios characteristic of endotherms (e.g., Bakker, 1974, 1977). Homeothermy could have been accomplished at first by increased body size and by the evolution of mechanisms to retard loss of the heat gained in exercise (McNab 1978). An increase of metabolic rate could have occurred separately. In the cynodonts, a group of advanced mammal-like reptiles, the presence of a secondary palate and the complex mastication apparatus both point to a high metabolic rate, requiring concomitant features enhancing the rate of food acquisition.

Most research (e.g., Crompton 1963; Crompton and Jenkins 1968, 1973) has focused on the changes in the jaw and dentition. This was partly due to their relatively good preservation and to the importance of dentition and mastication to the efficient processing of food required to service the mammalian lifestyle, which includes a high metabolic rate. The record of transitions – from the Pelycosauria to the Therapsida to the Cynodonta to the Mammalia – is impressive (Figure 6.32), as it includes a complete graded series ranging from the primitive reptilian skull with (1) alternate tooth replacement and relatively simple homodont teeth, (2) articular-quadrate jaw joint, and (3) relatively simple jaw musculature, to the mammalian condition of (1) single replacement of complex heterodont teeth, (2) dentary-temporal jaw joint, and (3) complex jaw musculature, which reduces the mechanical load on the articular-quadrate joint (Crompton 1963). A host of important features

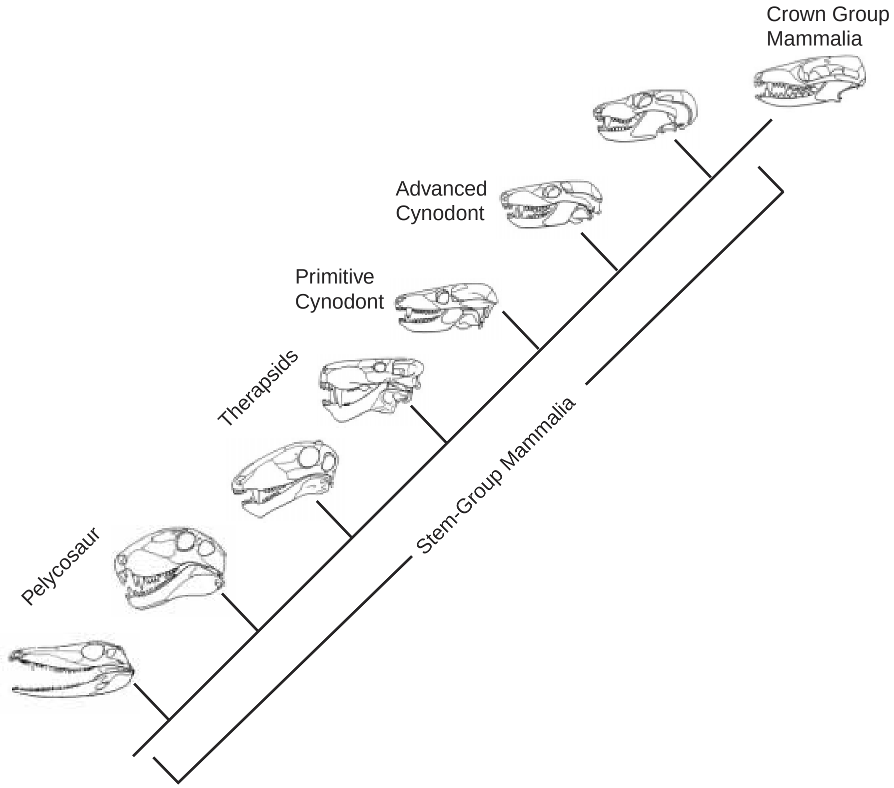

Figure 6.32. Some of the transitional forms leading to the rise of the crown group Mammalia. (Adapted from Sidor and Hopson 1998.)

evolve in concert with these three major systems, most notably the various muscular support structures such as the temporal fenestra (Frazzetta 1969).

The most interesting transition can be seen from the perspectives of jaw articulation and mastication. The evolution of efficient food processing requires complex occlusion and the ability to move the lower jaws in several directions (Crompton 1963). In the advanced cynodont *Thrinaxodon,* the postcanine teeth did not occlude in the sense of extensive intermolar contact. This was precluded by the reptilian tooth pattern of alternate tooth replacement (Crompton and Jenkins 1968). In more advanced cynodonts, occlusal facets essentially characteristic of the later mammals were established by gradual wear. Later, the faceting was genetically determined. Such changes in occlusion were accompanied by a change in the jaw musculature that permitted greater latitude in movement and increased mastication strength. Such strength would have exerted significant forces on the reptilian jaw joint, which functioned as a third-class lever. The evolution of the jaw musculature increasingly reduced the load on the reptilian jaw joint, and the opposing action of the temporalis and masseter muscles permitted the lateral control necessary for complex chewing. In the cynodonts, a trend for reduction of the postdentary bones eventually led to the possibility for the mammalian style jaw joint, which, in several transitional forms, existed in line with the older reptilian joint. This is the most unlikely transition of all: the coincidence of two fulcra (Jaanusson 1981). In modern reptiles and mammals, it would seem like an impossible transition for the location of a jaw articulation to switch from one fulcrum to another without a saltation.

In conjunction with this already remarkable series of changes, the evolution of the mammalian jaw joint is intimately involved with the evolution of the middle ear bones. The articular and the quadrate jawbones in reptiles are the homologues of two of the mammalian middle ear bones, the malleus and the incus (Hopson 1966). As the new mammalian dentary-temporal jaw articulation arose, the postdentary bones decreased in size and were freed for cooption as part of the middle ear apparatus. Allin (1975) argued that along with the trends in synapsid evolution toward masticatory efficiency, some features just anterior to the reptilian jaw joint indicate an auditory function. If this is true, then the evolution of hearing and chewing is an excellent example of Kemp's (1982) concept of correlated progression. From the point of view of functional morphology, this series of changes demonstrates that functioning structures cannot be predicted "from the ground up." To assemble a model of functional change, one must start with the reptilian joint and the constraint of a requisite for efficient hearing.

Our account of the changes occurring in the evolution of mammals demonstrates the complex interrelationships among the various parts of the skull, most notably muscular supports, dentition, and jaw articulations. The evolution of the mammalian middle ear (at least as we see it now) could not progress without significant change in the various features associated with the evolution of efficient chewing. It seems unlikely that any part of the skull could have evolved very much without an effect on the functioning of another. The best example is the need to reduce the mechanical load on the reptilian jaw joint, as masticatory forces become more intense and complex (Crompton and Jenkins 1968). Changes in the postcranial skeleton, the evolution of dorsoventral flexibility, for example, also helped contribute to the general need for an increase in food gathering efficiency. The latter was encumbered by still another evolutionary change incorporating higher metabolic rates that generate the need for a higher rate of food intake. As Kemp (1982) noted, it is difficult to take a modern mammal and dissect the crucial mammalian feature; all features are so interdependent. It is therefore not surprising and is rather gratifying to see the fossil record show a correlated progression of change.

This general account of transitional change[3] can be made more precise by defining the phylogenetic relationships of the various synapsid groups involved in the evolution of mammals with a cladistic analysis. We can then ask the question: Were the various mammalian characters acquired in independent groups, or can we speak of a correlated progression of features? Kemp (1982) associated the features acquired by the various groups with a cladogram depicting genealogical relationships.

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[3] In discussing the rise of the mammalian condition, we trace a line of descent through a very complicated cladal structure. As a matter of shorthand, it becomes convenient to say that "the synapsids gave rise to the mammals," but surely this must actually mean that "a species with the characters defining synapsids gave rise to a descendant bearing an additional character or set of characters defining the mammals."

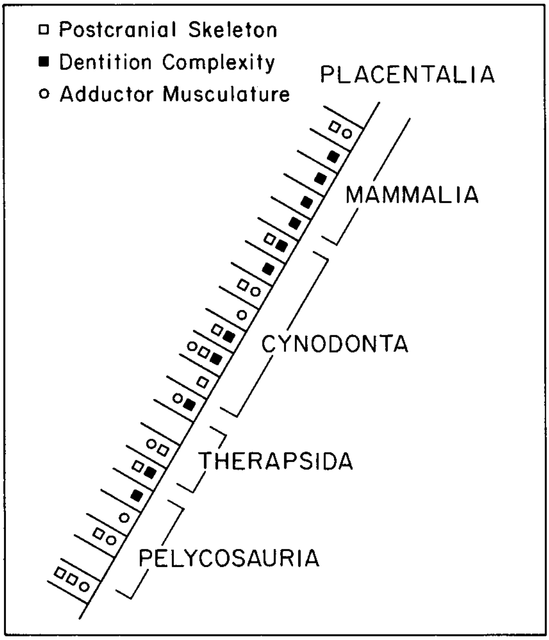

Figure 6.33. A cladogram for the genera in the lineage leading to the therian mammals. Major new acquisitions of skeletal features leading to the mammalian condition are indicated. (After Kemp 1982.)

Current data can articulate only the big picture; we have only a general cladistic skeleton and cannot say with the evidence whether transitions consist of minute quantitative changes or major qualitative changes. Intermediate morphological stages are usually absent below the family level, but the continual discovery of new forms suggests that missing data, rather than saltations, are the likely explanations. As an example, evidence until recently would have suggested a possible major quantum change, perhaps based on a developmental mutant, to explain the origin of the angular region of the mammalian jaw from the reptilian pseudangular process. But early mammalian fossil discoveries reveal an incipient process that might have been the progenitor of the angular region (Jenkins et al. 1983).

The pattern of acquisition of mammalian characters illustrated in the cladogram (Figure 6.33) shows the piecemeal nature of mammalian evolution. Significant incremental changes toward mammalness in the size of the jaw adductor musculature, complexity of the dentition, and the postcranial skeleton all occur in the majority of internodal steps in the cladogram. In the case of the interaction of jaw musculature, dentition, nature of the jaw joint, and the middle ear, these changes could not help but be interactive. Intermediate stages in the process are therefore functionally harmonious, the result of adaptation. Some other features, however, might have been acquired according to the model of mosaic evolution. The evolution of the kidney, for example, might have been in response to similar selective pressures posed by the terrestrial environment on feeding, but the acquisition need not be intimately correlated with changes in the skull. Sidor and Hopson (1998) quantified these transitional changes and found that (1) there was a significant correlation between stratigraphic order and position (ancestral vs. derived) on the cladogram and that

(2) the distribution of acquired derived traits appeared to be proportional to time, suggesting that there was no particular burst of morphological innovations concentrated at any one branch node. This confirms our qualitative impression of continuous gradational change in the origin of the mammalian crown group features.

As the record of the evolution of mammals is a story filled with intermediates, two important and unresolved questions come to mind:

1. Why did the process take so long – about 130 million years?
2. Is there any functional problem posed by intermediate forms?

The case of the mammals demonstrates that both questions, even if they have been major concerns in the history of evolutionary biology, may have little meaning when one considers organizational changes of this magnitude.

The question of tempo is nearly impossible to solve. We often forget that the complex of taxa involved in mammalian evolution had important and unique features other than those on which we focus in understanding the transitional stages leading to the mammals. In some cases, these unique features may have interacted significantly with intermediate character complexes and may have either led members of the taxon in question down a dead-end path or at least decreased the chances for evolution toward the mammalian condition.

For example, the dinocephalians constituted the majority of the early Late Permian therapsid faunas. They were large animals with a number of features that functionally may have precluded an easy advancement to the mammalian condition. Unfortunately, we have no idea as to how such conflicts might influence whether a group can be a progenitor of further advanced forms. In the context of terrestriality, there seems no doubt that the overall path toward the mammals involved adaptation, but other conflicting adaptations might have been present in many of the groups. Unless some clear model of selective value of these diversions and retardants can be established, it becomes fruitless to argue why the rate was so slow (or fast, for that matter). In many ways, the diversions are more interesting than the main mammalian line itself. Too often, we ignore the fact that many diverse creatures simply are precluded from being ancestors by being burdened with one or many features that restrict evolutionary direction and potential. It is therefore equally fruitless to view the evolutionary trend toward mammalness as "progress"; mammal-like reptiles didn't know what they were going to be, and true mammals do not remember what their ancestors were! Once mammalness was completed, however, it does make sense to ask why they have done so well with the array of features they have acquired over the past 130 million years.

The question of intermediate forms continues to be an intriguing issue because they are often absent in modern populations. Too often, an organism is chosen as an intermediate and an attempt is made to see what function its intermediate structures might have had. *Archaeopteryx* is probably the best example of such a transitional form. Because it is neither bird nor reptile, a believer in natural selection is often forced to make the case that the intermediate is functionally harmonious and could survive but was then inferior to either its ancestors or descendants and therefore lost out in evolution (e.g., Bock 1979; Simpson 1944, p. 92). Although this is plausible, it ignores the historical context within which the intermediate arose. *Archaeopteryx* was not half bird and half reptile. It was *Archaeopteryx*! It can be viewed as a mosaic of dinosaurian–reptilian and avian features, which is to say that it was an organism in its own right with a complex evolutionary and ecological history. Like the case of mammal evolution, the intermediate stages were integrated organisms with specific traits that were not passed on to distant descendants but might have enhanced survival in a particular milieu. Thus, although it is a fascinating and viable question as to exactly how *Archaeopteryx* used its feathers and forelimbs (e.g., Ostrom 1974), it is not clear to me that the fossil record is complete enough to expect that we will ever learn, for example, whether flight in birds started from "the ground up" or "from the trees down" without some extraordinary new discoveries or insight. Recent discoveries, at least, confirm Ostrom's theory of the derivation of birds from coelurosaurs but suggest that feathers arose without any enhancement of a potential for flight. There also is no great innovation in the origin of the clade Aves (Sereno 1999), which is consistent with the evolution of many other so-called baupläne, whose special status has been reified into special immutable taxa with unbridgeable gulfs between them. Indeed, there appear to be no special innovations in the origin of birds, because such characters as feathers and the "true avian" method of forelimb folding are to be found in sister groups of the Aves, with many other shared characters (e.g., Novas and Puerta 1997).

We might ask if this sort of gradual accumulation of characters, found in the broad picture of mammalian evolution, can be seen at lower levels, such as orders or families. As noted above, interfamily transitional forms are often absent, probably as the result of inadequate finds rather than saltation. But sufficient evidence exists to examine the question of whether evolution within a mammalian order is of the same type as on the level of Mammalia.

The mammalian order Carnivora first appeared in the middle Paleocene and was represented by members of the family Miacidae until the end of the Eocene, some 20 million years later. After the extinction of some coexisting carnivorous mammals, the miacids radiated into what produced most of the modern families of the Carnivora (canids, felids, viverrids, mustelids, ursids) as well as two extinct families. Using factor analysis, Radinsky (1982) demonstrated that the differences that now distinguish modern viverrids, canids, felids, and mustelids were less pronounced in the Oligocene, when these families made their first appearance in the fossil record. Cranial differences in representatives of the living families can be related to differences in prey killing but not necessarily to differences in prey type or size. But only some of these distinctive features can be found in Oligocene ancestors of the modern families. Radinsky suggested that body size differences established early in the history of the group might have been an important factor in the radiation. As body size is correlated to prey size in carnivores (Rosenzweig 1966), adaptations to prey handling might have been triggered by or coincided with body size differentiation. These adaptations might have been entrenched with the accumulation of further traits, when the miacids survived the Late Eocene extinction of many early carnivores, perhaps even as a matter of chance. From a quite different specific context, size variation in spores might have been the initial variation that was later evolved into morphologically distinct gametes and, ultimately, seeds in plants (Tiffney 1981). Heterospory is represented initially in the fossil record simply by spore size variation within a single sporangium in the Devonian *Chaleuria*. Thus, later complex morphological diversification might have been initiated by simple differences in size.

The evolution of the angiosperms provides another example of the piecemeal evolution common in the evolution of major new groups. As Tiffney (1981) noted, many of the features thought to be characteristic of the angiosperms were already present in their remote ancestors. Thus, if there is a feature such as "angiospermness," it arose not suddenly but rather by a combination of correlated progression and mosaic evolution. Tiffney outlined a scheme of potential correlated progression remarkably similar in approach to that of Kemp's analysis for mammals. Many of the individual features of angiosperms appeared in various fossil groups, but only one line seemed to accumulate them all. The appearance of angiosperms does not result in a geologically immediate explosion of evolutionary diversity (Sanderson and Donoghue 1994). The currently accepted ancestral line of angiosperms is depauperate in species, although this may relate to an as yet unknown extinction of an early radiation (Mathews and Donoghue 1999). More likely, however, it confirms the conclusion about the lack of an immediate radiation. Thus, not only are the origin and major diversifications of so-called new baupläne gradual but also their success is not inevitable.

Schindewolf (1936) was exactly correct. The first bird did hatch from a reptile's egg. But this is true only when we use some particular feature to define the birds. The class Aves was nearly already fully formed the moment it was "born." In some cases, the birth of a new group can be marked with a key innovation that must have permitted an extensive radiation. Do birds have such a key innovation? It may be found in the post-cranial skeleton, but feathers preceded the origin of flighted birds by many millions of years. An examination of the Carnivora reveals no keystone innovations that can readily define "carnivoreness" in one step (Radinsky 1982). The same can be said in the evolution of the mammals. Smith (1984) noted that the distinct nature of the extant echinoderm classes is not nearly so true in the Paleozoic. This has led to a spurious conclusion that ophiuroids and asteroids are the most closely related classes. Stebbins (1983b) briefly summarized the literature and reached the same conclusion of gradual assembly for the origin of birds, amphibians, and several other groups.

This discussion demonstrates, in some well-documented cases, that what we now consider a fixed bauplan in given groups of organisms arose gradually by accumulation of features that might or might not have arisen by correlated progression. In some groups, the doors to success were opened by key innovations, but this seems not to be the case for the mammals. This perspective, obtainable only from the fossil record, undermines a nearly essentialist viewpoint, which treats different baupläne as integrated entities that resist change, and tends to ignore their gradual origins. Gould stated (1983b, p. 80) that "the cluster of cats exists primarily as a result of homology, and historical constraint. All felines are alike because they arose from a common ancestor shared with no other clade. . . . All feline species have inherited the unique cat *Bauplan,* and cannot deviate far from it as they adapt." Genealogically, of course, all felids have descended from a common ancestral species; that is just restating ancestry and how cats are diagnosed in the first place. But this omits the essential nature of the evolutionary process. The "cat bauplan" was assembled gradually, first as "mammalness" and later as "catness." After this set of adaptations was congealed by both functional interactions and incorporation of traits into developmentally linked complexes, it is no surprise that current conditions do not now permit much of a deviation from the basic organization that we use to define cats. The entire process of adaptation and crystallization of the cat bauplan involved a presence in the same ecological milieu – that is, hunting, seizing, and eating usually mobile prey. In writing of present constraints, Gould led the reader away from the likely adaptive origin of cat traits. It is thus meaningless (loc. cit.) to dismiss correlations of cat morphology with the present environment and to argue that "genealogy, not current adaptation, is the primary source of clumped distribution in morphological space." How does one distinguish between genealogy and adaptation? The dichotomy is false.

The fossil record reveals a very clear pattern. From the lowest level of resolution of morphological change in phyletic lineages at the species level to the highest level, we see the gradual accumulation of novelties that contribute to form the distinctive and morphologically separate clades that exist today or have existed at any time in the past. The unique genetic properties of various traits strongly influence the pattern of change seen in a geological column. On higher levels, we see traits assembled over time and trait groups gradually congealing into total organisms with the evolution of various developmental programs. Some of these programs make any change very costly to the organism, but it is a matter for empirical investigation to determine this cost. But it is clear that the evolution of baupläne is often gradual and that the present distribution of groups tightly clustered in morphospace is in large part a reflection of this gradual congealing. Developmental constraints may regulate the congealing, but adaptation may often be a major element in the evolution of developmental constraints. Because the organism evolves mechanisms to stay in its favored environment, the gradual congealing is a reciprocal process of (1) culling of variants arising as mutants and (2) the increasing commitment of the organism to a given lifestyle that keeps it locked into the same selective regime for long periods of time. It is this very reciprocal process that weakens the claims for the isolated importance of historical or developmental constraints on evolution. Organisms adapt partially by sealing their own fates through a continually increasing commitment to a given lifestyle. As in the mammals, there is patent evidence that this increasing commitment is associated with improved performance. Adaptation is not divorced from history; it is an integral part of history.

Despite the host of mammal-like reptiles, and despite even the rise of the dinosaurs, the mammals prevailed. There is no special reason to believe that the dinosaurs became dominant owing to their superiority; rather, they probably filled the vacuum created by extinctions of nonmammalian synapsids and other groups (Sereno 1999 and references therein). This raises the question of whether intraclade superiority ever plays a role in the shift in dominance from one major group to another. In any such situation, there are two alternative explanations for success of the derived condition:

1. *Meandering route of evolution:* The sinuous path taken toward the mammalian condition produced a taxon with more survival value than its antecedents, which had relatively more ancestral character states for "mammalian" characters but also its own synapomorphies, which involved a unique evolutionary path on one side branch of the clade.
2. *Stochastic extinction:* It may be that all members of the clade happened to become extinct and the surviving one is falsely taken to be superior. In the case of mammalian evolution, the latter explanation is much weaker, for the advanced mammal-like reptiles had means of dealing with the terrestrial environment that were functionally superior to those of earlier forms. The net path to the mammals, moreover, contributed to the development of a functionally integrated phenotype that served the needs of efficiently finding and processing food. It is, of course, true that no given group in the main line of progression evolves for the sake of the ultimate and most progressive form, but the latter could not have arisen without the appearance first of the former.

Cladogenesis may hasten the advancement toward a derived condition, as in the case of mammalness. Consider a single phyletic lineage, acquiring gradually the specializations necessary to achieve the mammalian condition. At any one time, the taxon will have a given set of ecological restrictions and will therefore have limited opportunities for novelties to arise from the extant morphological material and the ecological exigencies that challenge the populations. But if cladogenesis occurs, it is likely that more types of environments will be encountered by the group, and that more particular adaptations may bring the total group into exposure with a larger range of ecological challenges. This may hasten the chance that one of these taxa, assuming all have the same degree of mammalian advancement, will encounter the situation that will lead to further progression. Cladogenesis, therefore, does probably hasten the rate of progressive evolution. But this process fits the notion neither of directed speciation nor of species selection, because we are still considering a core path of progress that leads to the derived and advanced state. It is not speciation per se but phyletic evolution in the isolated lines that results in the fixation of given novelties. Cumulative change may thus be hastened by cladogenesis.

The arguments presented above view trends in evolution as the result of complex adaptations acquired mainly by phyletic evolution. In the case of the mammals, the functional integrity of the many observed evolutionary changes strongly argues against the model of punctuated equilibrium and species selection. There is no compelling evidence that phyletic evolution is insufficient to generate and congeal the series of successively acquired novelties that eventually comprised the mammalian condition. Whereas, as mentioned above, cladogenesis increases the chance of encountering more opportunities for new character combinations and new ecological situations, the line leading through to the mammals can still be viewed as a sinuous phyletic path. Selective extinction may easily, of course, be the reason why the mammals are around today, and the pelycosaurs and therapsids are only history. But the cumulative evolution of traits leading to the mammals is an excellent case of complex adaptation that requires no decoupling of within-species versus among-species processes, as suggested by Stanley (1975).

The species selection model (Eldredge and Gould 1972; Stanley 1975, 1979) argues that speciation generates a series of morphologies that are random with respect to a trend, and that selective extinction determines the trend. This can hardly be argued very seriously in the case of the mammals or in other groups in which integrated functional morphological complexes can be readily identified (e.g., Miyazaki and Mickevich 1982). In such cases, random generation of morphologies about a trend seems functionally absurd (Levinton and Simon 1980). In the mammals, change can be visualized only in highly restricted directions, given the constraints of facial muscles, pressure on the jaw joint, and the overall selective pressure of terrestriality. Stanley (1979) suggested the possibility of directed speciation, in which species arise only in a morphologically biased direction. But this only associates tautologically a phyletic pattern of evolution with a series of species delineated strictly and arbitrarily by morphological changes. In principle, nothing excludes species selection from being an important aspect of evolutionary trends. At present, however, there is no strong evidence for the general importance of the process, and it certainly is not necessary, given the possible rates of phyletic evolution.

Could it be that many independent lines of evolution toward the mammalian condition could have developed but that random extinction spared all but one or a few? This alternative still begs the question of the likely directional progression of all the independent lines in the first place. Although some minor features might have been different, the major trends toward homeothermy, processing of food, and efficient locomotion would probably have been solved in similar ways. Therefore, a somewhat different type of mammal might have arisen if history, in the form of extinction, might have been somewhat different, but similar constraints on phyletic evolution would have led in predictable directions. A possible example of a different outcome might be imagined for the evolution of the bones of the mammalian middle ear. Somewhat different directions of evolution might certainly have resulted if other bones had been exapted for hearing.

The German paleontologist Rudolf Kaufmann (1933), in his studies of evolution within the Upper Cambrian trilobite genus *Olenus* in Sweden, articulated the concept of *Artabwandlung,* whose meaning might be conveyed by the phrase *intraspecific directional modification* (see Teichert 1949, p. 49). The four stocks all show similar phyletic trends in size, shape and ornamentation, which can be seen partially in Figure 6.14. Here, where some definitive evidence exists, it is clear that phyletic trends within elements of the clade can be seen as the net evolutionary trend of the entire clade. This situation is by no means unique. In the evolution of the horses, trends toward hypsodonty and monodactyly can be seen in many lines, particularly in *Cormohipparion, Hipparion, Neohipparion,* and *Nannippus* (MacFadden 1985; Simpson 1951; Woodburne and MacFadden 1982). In this latter case, the process of *Artabwandlung* can be placed in a context of functional morphology. These examples suggest that there is nothing compelling about the species selection model, because net trends seen for the whole clade are duplicated within phyletic lines. History might be slightly different in the different lines, but functional constraints provide an important predictable guidance to the directions of morphological evolution. In some cases, the continuing interplay between the rise of new structures and functional constraints may make for a host of unique solutions; in these cases, interclade extinction might play a very important role in the group that finally "wins out." This would be an intermediate, and acceptable, position between those who believe in either the primacy of phyletic evolution or species selection in adaptive trends.

Kaufmann's concept of *Artabwandlung* corresponds to Vavilov's (1922) law of directed series. Vavilov argued that when representatives of related taxa are placed in similar environments, similarity of biology would result in similar reactions. Thus, adaptive evolution in parallel lines may result in similarity of form, owing to a similar "predisposition," which might include a variety of genetic and developmental constraints. Unfortunately, we are only at the beginning of an understanding of the relationship of functional, genetic, and developmental integration. Nevertheless, an important principle emerges from this discussion – it is the trend that matters. Large-scale trends are telling us something, but we must be able to filter out the noise. The trends seem like they may be unexplainable in terms of neo-Darwinian evolutionary change, until we place the taxa on a tree and trace the thread. There is no purpose or objective in this sinuous path that led, for example, to the mammalian condition, but it is adaptive, nevertheless. Larger-scale taxon sorting matters to the degree that various contingencies placed taxa in environments that contributed to the overall progression, but we have no real idea of how to separate neo-Darwinian evolution from sorting, except perhaps in small instances.

The story of horse evolution is a classic in adaptation and macroevolution, which we owe to the great work of George Gaylord Simpson and his successors. Simpson recognized that horse evolution could be described only as a complex radiation, but many lines shared a trend toward hypsodonty, which is a response to the wear on teeth during feeding, particularly grazing on tough grasses. For horses, hypsodonty involves ever-growing and high-crowned teeth (MacFadden 1992, p. 233). From the Eocene to the Early Miocene, horses had short-crowned teeth, which corresponded to a browsing habit, but the expansion of grasslands in the Miocene resulted in a rapid radiation of horse lines, each of which developed more and more hypsodont teeth. A change from clayey soil to sand from the Oligocene to the Miocene might also have been a selective force for hypsodonty (MacFadden 1992, p. 235).

Mammalian herbivores can be broadly classified as browsers or grazers. Tooth wear comprising more scratches and fewer pits is associated with grazing, and the complementary pattern identifies browsing. Also, differences in $\delta^{13}C$ between browse plants, dominated by C_3 (Calvin) photosynthesis, and grazed grasses, dominated by C_4 (Hatch–Slack) photosynthesis, are reflected in isotopic deviations found in mammalian teeth. Using living mammals as a guide, Miocene–Pliocene Bone Valley horse species spanned both feeding types, and some of the most hypsodont horses appear to have mainly browsed (MacFadden et al. 1999). It is perplexing that one of the least hypsodont species, *Nannippus minor,* was principally a grazer, at least by virtue of wear and stable isotope evidence. The only survivor of the group of coexisting horse species was strongly hypsodont.

This example challenges us in many ways. First, a broader perspective suggests that hypsodonty is not so faithfully associated with the grazing–browsing alternative. Llamas and gazelles are not primarily grazers, yet they are hypsodont. Baboons and kangaroos, although primarily grazing, are not especially hypsodont. We can escape this trap by rejecting Simpson's simple association between hypsodonty and grazing, but we cannot ignore the trend toward hypsodonty observed in the Miocene as grasslands expanded. A disturbing conclusion emerges: Morphological trends might be readily explainable by adaptation, but no particular set of species may be uniquely explainable in terms of absolute values of a particular morphological trait relative to the microenvironment in which the species finds itself. Another way to say this is that we can see a selective force at work when change is occurring, but a snapshot of coexisting species may be harder to interpret. Again, it is the trend that matters.

There is one sense in which major trends might be the result of species selection, but not of the sort suggested by previous authors. The more different types of descendants produced, the more possibilities there might be for movement along a major trend of complex evolution to proceed, such as evolution of the mammalian skull and associated traits. Thus we might imagine one clade being trapped in a cul de sac, while another has a morphological configuration with variation capable of selection and evolution along a general trend. As a hypothetical example, it might be that the mammalian condition of tooth replacement is unlikely to evolve when simple teeth are selected, say in a clade adapted to simple seizing and swallowing of prey. Another clade, adapted to folivory and frugivory, might have stronger selection for complex occlusal surfaces. Thus the more clades generated, the higher the probability of acquiring dentition more consistent with rapid processing of food, which might be of selective advantage in a form with higher metabolic rate. This line of reasoning, which probably is filled with specific difficulties (I am an invertebrate biologist, after all!) would suggest a higher level of Fisher's Fundamental Theorem: that evolutionary trends are more likely to proceed if there are more clades upon which natural selection and phyletic evolution acts.

The Main Points

1. In large measure, the incompleteness of the sedimentary and fossil record strongly biases our perception of evolutionary processes, especially the spectrum of evolutionary rates.
2. The completeness of the sedimentary record depends on the desired temporal resolution. For short periods of time, such as 1,000 years, most intervals will not be preserved in a geological column. This effect is so pronounced that sedimentation rate appears to be related inversely to the overall period of time represented by the geological column. Periods of interest to students of speciation and population genetics can be shown to be poorly sampled by most geological columns.
3. Most estimates of evolutionary rates seem paradoxically slow and could be explained by genetic drift. This paradox seems related to the underrepresentation

of many short spans of time, when rapid rates of evolutionary change could be delineated. The longer periods of time typically sampled by paleontologists combine periods of rapid evolution, reversals, and no change. As a result, evolutionary rate appears to be inversely related to the time period represented by the geological section, much as is found for estimates of sedimentary rates.

4. The punctuated equilibrium theory asserts that the major part of a species history is characterized by stasis, and that evolutionary change is usually concentrated in speciation events. Most discussions of stasis, however, focus on change in individual characters. The coarse time resolution of most fossil studies biases us toward a perception of stasis.
5. Because species are identified only by morphological difference, the association of speciation with morphological change is usually a tautological exercise. This is especially true in studies in which there is no evidence for cladogenesis, yet speciation events are documented by sudden morphological change. Given the limitations of species identification and the timescale resolution of the fossil record, the punctuated equilibrium theory cannot usually be tested in the fossil record. By now, however, at least a couple of cases exist that seem to fit the requisites of the punctuational model. More impressive are the many more examples of gradual tranformation of lineages.
6. It is possible to test for the efficacy of character change. By now, a large number of studies demonstrate the common occurrence of phyletic evolution of a sufficient magnitude to produce change on the order of specific and generic differences. The variety of population genetic mechanisms affecting evolutionary traits and the range of genetic mechanisms controlling traits make it fruitless to look for the pattern of stasis and ascribe it to any particular process. There are a few well-documented cases of long-term stasis, particularly for shelf invertebrates. Mammals and marine protists seem to have common directional phyletic trends.
7. There is little fossil evidence giving us insight into the origin of major new body plans. The accumulated evidence for the evolution of the mammals suggests that a series of adaptations were acquired gradually and piecemeal. The origin of the mammals seems to have involved the interplay of a variety of ancestral constraints (e.g., the osteological configuration of the reptilian skull) with adaptive changes that improved performance in a terrestrial environment.
8. Snapshots of species with traits inevitably create confusion, owing to the complex histories that precede their evolution, appearance, and survival of past extinction. Adaptation can be understood only in the context of evolutionary trees and trends mapped on the trees.
9. A macroevolutionary analogue of Fisher's Fundamental Theorem of Natural Selection can be postulated. When more descendant clades are produced, there are more opportunities for phyletic evolution to move along toward a path that ultimately results in a general evolutionary adaptive trend, such as the evolution of the mammalian skull.

CHAPTER 7

Patterns of Diversity, Origination, and Extinction

> The sea lost its serenity.
>
> – Y. Mishima, *The Decay of the Angel*

Introduction

A paradox arises from the large-scale perspective afforded by the fossil record. Phyletic evolution and adaptation appear to be ubiquitous; yet adaptation cannot always be equated with success, relative to coexisting but supposedly inferior forms. The rise of vagile shell-crunching predators in the Mesozoic was accompanied by an expected overall mechanical resistance to predation in the marine benthos (e.g., Vermeij 1977, 1983). But the response may be necessary and not sufficient to explain the many evolutionary radiations that occurred during the Mesozoic. Can we explain ammonite diversity from the point of view of predation alone? It is likely that invasion of a wide variety of habitats and lifestyles contributed more to ammonite diversity. Did the ammonites proliferate because of individual adaptation? If so, why have they not stood the test of time and survived to the present day?

The dinosaurs proliferated in the Mesozoic, coexisted with mammals for many millions of years, but eventually gave way to the mammals in the Cenozoic. Are the dinosaurs to be considered inferior to their ecological successors, the mammals? If so, one has to explain why the mammalian condition, when achieved in the Triassic, took over 100 million years to manifest itself in worldwide dominance in the early Cenozoic. Why did the dinosaurs fail to succumb immediately, if the mammals were so superior? The great time period involved in the gradual evolution of "traits" such as mammalness also invites difficult questions. How can such an overall development transcend the Carboniferous–Triassic time span, which included the greatest biological catastrophe – the Permian – of the Phanerozoic?

Some might argue that the issue of success is mired in the definition of taxa. After all, unless recent evidence undermines the conclusions of a number of investigators, birds were derived from theropod dinosaurs. One might make the claim, therefore, that the dinosaurs never became extinct and the monophyletic dinosaur–bird group is very successful today. Such a point of view highlights the conflict between Simpson's original notion of groups as major adaptations and the cladistic notion of groups being defined only on the basis of monophyly. Which point of view do you choose when it is clear that dinosaurs are a paraphyletic group yet are phenotypically distinct?

It isn't clear that we can ever answer these questions, but a biologically meaningful history of the earth is essential as the historical backdrop for major evolutionary events. To do this, we have to have means of enumerating taxa, their stratigraphic ranges, and biogeographic distributions. We have seen from our discussion of form and function that history plays a key role in the nature of the adaptive process. We must know how the organism's past history shapes its reaction to its present environment, but we must also know how the immediate environment imposes itself on the organism.

Paleontologists have mainly used the presence of the fossil organisms themselves as the principal evidence of the relevant events in earth's history. The sudden and simultaneous disappearance in geological sections of groups of species was the basis for the catastrophism of Cuvier in the eighteenth century, and the nature of mass extinctions still figures prominently in current debates about the biological history of the earth. Major turnovers in fossil biotas are often far more distinct than associated physical evidence, which may involve indications of retreats of the sea, arrangement of the continents, or changes in climate that may also occur with no extinctions. The fact of the turnover is much easier to establish than the causal factor, whose exact identification can usually only be vaguely inferred by means of imperfect correlations. Even in the cases in which obvious correlations occur, it is not usually clear whether the change is "important" enough to induce the change in the biota, without the post facto establishment of the correlation with an extinction.

Extinction is the province of the paleontologist. We believe that we are now possibly living through a mass extinction caused by human disturbance of high-diversity habitats. But we know very little about the extinction of species, except by fairly obvious mechanisms such as hunting. Can knowing that the dodo or the passenger pigeon was hunted to extinction help us very much with understanding the broad sweep of geological time? I doubt it. Additionally, invasions have caused extensive extinctions on oceanic islands (Pimm, Moulton, and Justice 1994), particularly when alien predators overwhelm small populations of endemic species (Hadfield, Miller, and Carwile 1993). Unfortunately, the timescale for larger-scale changes is probably unapproachable by the neontologist, who can observe only "normal" extinction (Diamond 1983), and we don't have much understanding of what occurs normally. It may be that fine-scale studies of the fossil record may eventually give us more insight into species-level extinction than neontological studies ever will. After all, the durations of animal species range from the order of 10^5 years (mammals) to 10^6 to 10^7 years (Raup 1991). Even with millions of living species, we are not likely to be able to document many cases of typical extinction of living animal species. The fossil record is probably our only hope.

The only conceivable interface between living and fossil systems might be achieved by studying the species-area effect. Ecologists have long recognized that the number of species is characteristically related to area, by means of an exponent of less than one, usually between 0.2 and 0.3 (MacArthur and Wilson 1967). This relationship, found both on islands and continents, may reflect processes involving a balance of immigration and extinction (in the case of islands) or speciation and extinction (on continents). Over geologically significant periods of time, such a balance may be integrated with other processes to explain trends in diversity (Levinton 1979). We will discuss this further below (in the section entitled Steady-State Levels of Taxon Richness).

To examine larger-scale changes, we are best served by having the tools of the geologist at our disposal. What do we know about such large-scale patterns? Paleontologists are best at recognizing given taxa by diagnostic characters, usually of taxa above the level of species. They can also establish an approximate date of occurrence, diagnose facies (rock type indicating the overall environmental regime), and paleogeographic location, which allows us to collate a series of snapshots of the biotic character of the earth at various times and places. These pictures taken together reveal the following general patterns that must be important in our explanations of macroevolution.

1. Correlated origins of different clades
2. Correlated diversifications of different clades
3. Near simultaneous extinctions of groups seemingly unrelated in ecology or genealogy but often co-occurring in the same habitat type
4. Replacement by ecologically similar forms after extinction
5. Occasional long-term constancy in the morphological types and quantity of coexisting taxa, despite some degree of turnover

These patterns appear at many levels of time and taxonomy. It is the purpose of this chapter to discuss the quality of the overall evidence for these generalizations and their explanations.

The Quality of the Data

Broad-scale trends in taxon richness usually derive from a complex database produced by many workers using different systematic methods and collecting techniques, and encountering variable modes of preservation. Such inherent problems raise substantive issues as to whether it is possible to infer any clear patterns through the haze of potential collecting and preservational biases. Worse than that, some of the biases may generate mistaken impressions of diversity change. As we will see below, some disagreements over major historical events turn around interpretations of potential sampling bias.

The taxic approach. We mentioned in chapter 2 some of the problems that an unevenly applied systematic philosophy creates in the interpretation of the fossil record. A taxon can be assigned a given rank by virtue of its species richness, phenetic difference from other taxa, or phylogenetic relationships with other taxa. No standard can relate a given taxonomic level of one group with another, although criteria that are internally consistent within a group might be imagined.

In studies of changes of taxon richness over time, the problem of bias becomes more complex, as the number of species is often the objective, but usually taxon richness can be easily assessed only at some higher level (e.g., families, orders), because fossil species are notoriously difficult to identify. This is particularly a problem, as it is well known that certain taxonomic levels are "natural" for one group but rather arbitrary for another. In principle, it ought to be possible to calibrate a given taxonomic level against the species level by using taxon-to-species ratios appropriate for the time period (see Van Valen 1973a).

Changes in ratios of one taxonomic level to another might thwart any estimate of species richness by means of surrogates like higher taxonomic units. The ratio of orders to families decreases significantly from the Paleozoic to the Mesozoic (Sepkoski 1984). Thus, a previous report of a long-term steady-state level of ordinal diversity (Sepkoski 1978) becomes ambiguous in interpretation. Does it represent species richness (species diversity aspect of taxonomic rank) or temporal constancy in the degree of morphological diversity (phenetic diversity aspect of taxonomic rank)? Similarly, the ratio of families to species decreases by a factor of two from the Mesozoic to the Cenozoic (Valentine 1969; Sepkoski 1984). An additional problem is the asymptotic climb of numbers of families as a function of increasing species numbers. During a modest extinction that is random with respect to families, the number of species becoming extinct will be underestimated if a linear relationship between families and species is mistakenly assumed.

The acuteness of the problem becomes still more obvious when we consider more detailed data. Rowell and Brady (1976) followed the diversification in a Cambrian biomere, which represents one of several iterative radiations of marine benthic trilobites from cooler-water Olenid progenitors (Palmer 1984). In the case of the polymeroid trilobites, an increase of generic richness correlates well with species richness. In the inarticulate brachiopods of the American Cordillera, however, species increase in number, but the number of genera remains constant. If the tabulation were reported on the generic level alone, we would have a far different picture than that expected for species.

The nature of taxon identification can introduce strong bias in estimates of appearances and extinctions. Because taxa, especially at higher rank, are often defined by phenetic distance, it is common for taxa to be paraphyletic, that is, to be identified by ancestral rather than shared derived characters. With paraphyletic taxa you can mistakenly count a lineage as going extinct, when it actually has surviving members, which may lead to an underestimate of extinction. Some have argued that this might lead to inappropriate estimates of extinction rates (Patterson and Smith 1987). The simulations of Sepkoski and Kendrick (1993) demonstrated that incomplete preservation in the fossil record sometimes confers an advantage upon the use of large paraphyletic groups, mixed with smaller and derived monophyletic groups. With incomplete sampling, at least some taxa are preserved, if varying criteria are used to define taxa, because some taxa will be retained that might define some aspect of the biota. Robeck, Maley, and Donoghue (2000) simulated origins and extinctions and found that the use of a range of sizes of taxonomic groups (including different numbers of subordinate taxa, such as genera) tended to capture the most appearances and extinctions in incompletely preserved biotas. On balance, it is not always clear whether monophyletic or paraphyletic taxa or a mixture do better to estimate extinction rates in cases of incomplete preservation.

In estimating diversification rates, monophyletic taxa are always preferable (Smith 1994). For example, it seems to be useful to estimate branching rates between sister taxa, because the difference in branching rate can be related temporally and phylogenetically to a single node on a tree. Implicitly, this approach is taken in the study of the role of key innovations in the diversification of a clade, as discussed in Chapter 5. Unfortunately, statistical analyses to test for differences in diversification are difficult to apply (Sanderson and Barathan 1993).

Another important source of bias is the distribution of individuals among taxa. In many diverse fossil groups, such as the ammonites, a large proportion of all named species may be defined and encompassed by a single specimen. Naming species rampantly in this way tends to artificially reduce their geological range, which increases the impression of strong turnover (proportion of taxa appearing and becoming extinct within the same time unit). Thus strong turnover may just be a biased representation of oversplitting of taxa.

Preservational biases. Paleontology students quickly learn that fossil collecting is as much art as science. The struggle usually is to take uneven access to localities, variable preservation, and sometimes poor sampling geographically and to nevertheless come up with a convincing characterization of geological range, paleobiogeography, and microhabitat distribution. Geological sections rich in fossils are common but are usually not available in a form ideal for random statistical sampling. Although models incorporating inhomogeneities of preservation are possible (Marshall 1997), a complete accounting of the temporal and spatial distribution of preservation gaps and variation in preservation probability is likely to be rare. Of course, not all gaps in fossil occurrence are due to poor preservation. Many paleoecological studies have demonstrated that sporadic occurrences often represent the uneven presence of suitable microenvironments or episodic colonization by species with rapid colonization potential (Levinton 1970). This further complicates models accounting for variations in fossil occurrence. The student is nevertheless confronted with obvious cases of preservational bias. In coastal plain sediments of the middle Atlantic states, obvious zones of poor preservation of molluscan faunas can be correlated with solution by groundwater; immediately adjacent areas will show good preservation in sediments with identical texture and degree of burrowing. In the nearshore clastic sediments of the Upper Cretaceous of New Jersey, one side of a hill may yield internal molds of gastropods and oysters, whereas the other will lack such molds but bear great abundances of oyster shells.

Differences in fossil shelly faunas can be due to the stricter set of conditions often required to record the presence of animals with aragonite shells (most gastropods), as opposed to calcite (oysters). As a result, especially well preserved bivalve coastal plain fossil faunas have a decided peak in richness, relative to other localities. This may lead to spurious beliefs in strong endemism, where unusually fine preservation is the actual cause of the unique occurrence. The Owl Creek Formation in the Cretaceous of the Gulf Coast, for example, has a malacofauna enriched in well preserved and aragonitic forms. Its endemism was halved once the nearby Providence Sand was taken into account (Koch and Sohl 1982).

Although gaps are common, it is surprising how closely death assemblages, at least of preservable skeletal macrofauna, can resemble living assemblages in the same sediments. Death assemblages are typically more diverse than reports of living assemblages, but this usually derives from the short-term representation of the living fauna, whereas the death assemblages time-average more environmental variation of the past few years to decades (Kidwell and Flessa 1996). Variations in preservation in the record probably mainly stem from wholesale lack of preservation or perhaps uneven colonizations of habitats by opportunistic species assemblages (Levinton 1970).

Preservational biases may make strange bedfellows of species that normally do not occur and may even be ecologically incompatible. Subtidal muds of southern New England are often dominated by polychaetes and bivalve mollusks, but the skeleton-bearing clams are the only likely candidates for long-term preservation as fossils. Muds that have not been disturbed by episodes of sedimentation or pollution are likely to be dominated by the protobranch bivalves *Nucula annulata, N. proxima,* and *Yoldia limatula,* with occasional dominance by the tellinid *Tellina agilis*. But ecological disturbances often bring on enormous densities of the small mactrid bivalve *Mulinia lateralis,* which spreads by means of planktotrophic larvae, can live under anoxic conditions for many days (Shumway 1983), and reaches the age of reproduction in only about 60 days, which is very unusual for bivalve mollusks (Calabrese 1970). In terms of habitats, one can visualize southern New England subtidal muds as a mosaic of disturbance-dominated bottoms and sediments that, although undisturbed for some period of time, move toward deeper-burrowing species and dominance by the protobranchs. Thus, *Mulinia lateralis* is not expected at any one place to co-occur with high densities of protobranchs.

This story of horizontal lack of co-occurrence is not duplicated in vertical cores taken in Long Island Sound (Levinton and Rhoads 1974; Figure 7.1). Whereas *M. lateralis* and protobranchs are spatially negatively correlated at the present time, they are positively correlated in abundance with vertical position in a core. This seems paradoxical until one appreciates that temperate silicate muds have conditions conducive for shell dissolution and protobranchs have relatively little calcium carbonate per unit mass of organic matrix. This is not so for *M. lateralis*. Thus, when *M. lateralis* invades and becomes very abundant, microspatial chemical conditions are dominated by calcium carbonate shells, which creates a buffering effect. In this microenvironment, *Nucula* and *Yoldia* shells are preserved more readily than in the intervening stratigraphic levels of the core where protobranch shell-dominated sediments are conducive to shell dissolution (i.e., no fossilization). Thus, a positive correlation misleads as to ecology and abundance in life.

Preservational bias may operate on the grand scale of the Phanerozoic. Valentine analyzed family-level diversity of "well-preserved" marine invertebrates throughout the Phanerozoic and noted a Middle Paleozoic high, a Permian low, and a post-Permian expansion. Raup (1972b, 1976a, 1976b) tabulated species richness from the *Zoological Record* and obtained similar results. But he also found a strong positive correlation between species richness and estimated world rock volume for given geological periods and found a positive correlation on a smaller geographic

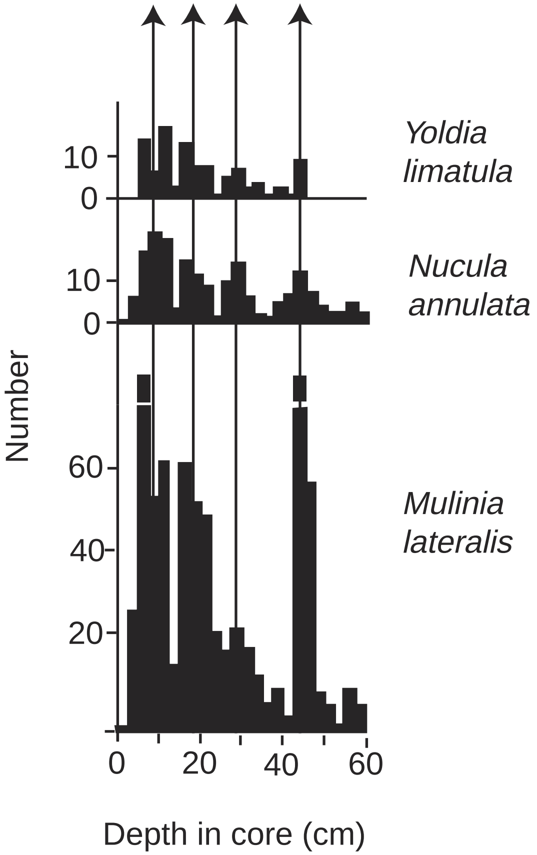

Figure 7.1. Diagrammatic representation of actual abundance over time in Long Island Sound of the opportunistic bivalve *Mulinia lateralis* and the bivalve *Nucula annulata,* which lives in more environmentally constant conditions. Right, preservation in the fossil record, as recorded in cores.

scale using Canadian occurrences. Tiffney (1981) reported a positive correlation between nonmarine outcrop area and species richness of fossil plants. These correlations are worrisome and raise the possibility that all patterns of species richness in the record might be artifacts of preservation. However, if the statistical contribution of rock volume is subtracted, a significant residual pattern of relationship between area and species richness remains (Sepkoski 1976). Moreover, a comparison among very different data sets based on global and local taxon richness all have yielded a similar temporal pattern of overall taxon richness (Sepkoski, Bambach, Raup, and Valentine 1981). Most significant are the changes of within-community diversity, which parallel the broader trends (Bambach 1977; Niklas, Tiffney, and Knoll 1979; Tiffney 1981). This suggests that the qualitative pattern is real, but that care is required in the interpretation of taxon richness trends.

Although the overall change of diversity in the Phanerozoic may not be due to a bias created by fluctuations in preserved sedimentary rocks, smaller-scale changes in sedimentary preservation diminish a clear understanding of crucial periods in the history of life. The end of both the Permian and Cretaceous are believed to be crisis periods for the world biota. But both time periods are marked by extensive regressions of the sea, with concomitant reductions in rocks recording events of those times. In the Permian, the problem is so severe that many groups seem to become extinct, only to reappear, like Lazarus, in the Triassic, when appropriate environments are preserved to a greater extent. The end of the Cretaceous is marked by a widespread erosional gap that precludes detailed study of biotic declines but also creates the illusion of a disappearance of entire biotas, where none might have existed (Kauffman 1984; Newell 1967). Marine regressions reduce the amount of sediment deposited, which concomitantly reduces our sampling power of fossil taxa. A gradual regression, therefore, could make the number of shallow-water species appear to diminish gradually, even if an extinction event were, in fact, sudden. Rare species, whose range is poorly sampled, would appear to disappear before their actual extinction, because their actual time of extinction would likely be poorly resolved (Signor and Lipps 1982). An estimate of temporal stratigraphic completeness suggests the unlikelihood of distinguishing episodes of extinction lasting 100 years or less from those lasting as long as 100,000 years. Sudden catastrophes would therefore be impossible to document with our stratigraphic record (Dingus 1984). The combined effect of rare species giving a wrong impression of earlier extinction and the problems of poor sampling owing to less rock volume has been termed *backward smearing,* as a sharp extinction is effectively rendered into a fuzzy decline.

The fossil record is biased toward readily preservable forms with hard, mineralized skeletons. Most studies of fossil taxon richness therefore tend to include only those taxa that are liable to be consistently well preserved (e.g., Flessa and Imbrie 1973; Valentine 1969). The vast array of soft-bodied forms are usually absent, making any attempt to completely understand the record of groups such as annelids essentially hopeless. But what is the overall quality of the record of those forms that have skeletons and are found fairly commonly? The very fame of *Archaeopteryx is* testimony to the absence of a record of the majority of early avian evolution, although some spectacular finds have dotted the journals in recent years. Many embarrassments of preservation exist, such as the very long gap between living Monoplacophora and their most recent relatives, and the living occurrence of *Latimeria* despite an immense temporal gap between it and any close relatives. The "pull of the Recent," as Raup (1978) described it, enhances the chance that poorly preserved fossil taxa will appear in the – by definition – perfectly preserved and better-sampled living biota, with no close fossil relatives. Combined with better preservation and comparatively easy identification of younger Cenozoic fossils, there may be a false sense of rapid increase of taxon richness as we approach the present.

Occasional sites of extraordinary preservation, the so-called lagerstätten, lend insight as to the degree to which the fossil record faithfully records even the skeletonized taxa. The Burgess Shale is a particularly extraordinary window on the Middle Cambrian, and we will discuss it at length in chapter 8. It was discovered quite accidentally in 1909 by Charles D. Walcott in the Canadian Rocky Mountains near Field, British Columbia, Canada. A series of publications was followed by a later reinvestigation led by Harry B. Whittington (see Conway Morris 1979). The fossils (see Figure 8.4) are usually thin films on shale bedding surfaces and mainly consist of arthropods and their allies, including trilobites, the onychophoran *Aysheaia pedunculata,* and a host of arthropods with no apparent close living relatives. A suite of echinoderms, mollusks, brachiopods, polychaetes, and priapulids, among others, are also present. The whole assemblage was probably representative of one overall habitat type, though more recent studies suggest a series of distinct biotic reef-front assemblages (Collins, Briggs, and Morris 1983). Although the vagile trilobite epifauna is fairly similar to other less well preserved communities, the vagile infauna – dominated by burrowing priapulids – and the sessile epifauna – often dominated by probable sea pens – are both indicative of an overall preservational problem for ecologically significant groups in this time and environment. These groups are widespread in rocks of the immediate region and are not a peculiarity of one local site (Collins et al. 1983). The bias is therefore quite serious. If the unusual forms are subtracted from the overall fauna, however, the residual of typically fossilizable groups closely resembles Middle Cambrian shelf assemblages. The residual, therefore, at least represents a core of fossil material that is consistently represented through various states of preservation. Bits and pieces of the Burgess Shale fauna appear in the Wheeler and Spence Shales of Utah and even the Lower Cambrian Kinzers Formation of Pennsylvania. Both comfort and discomfort are therefore imparted by such unique windows into the past.

In accounting for broad-scale changes in taxon richness, we must have an idea of the proportion of fossil taxa that have been preserved for us to count, which we define as *taxon completeness*. Our data (Figure 7.2) usually consist of a series of time bins, stacked to produce a geological time stratigraphic unit. The range may be complete, but more likely occurrences will be found in only some of the bins, and often discontinuously. The true duration may be greater than the fossil range. Foote and Raup (1996) assumed an exponential distribution of true durations, which permits a simple estimate of taxon completeness, based on the frequency of taxa with observed ranges of one (f(1)), two (f(2)), and three (f(3)) intervals, respectively (see also Solow and W. Smith 1997). The preservation probability R is

$$R = f(2)^2/[f(1)f(3)]$$

This, when combined with the recovered distribution of actual fossil durations, allows one to calculate the proportion of taxa that are preserved. The results are encouraging (Table 7.1). Taxon completeness for Upper Cambrian–Lower Ordovician trilobites, for example, is about 0.9. Other groups are often as good.

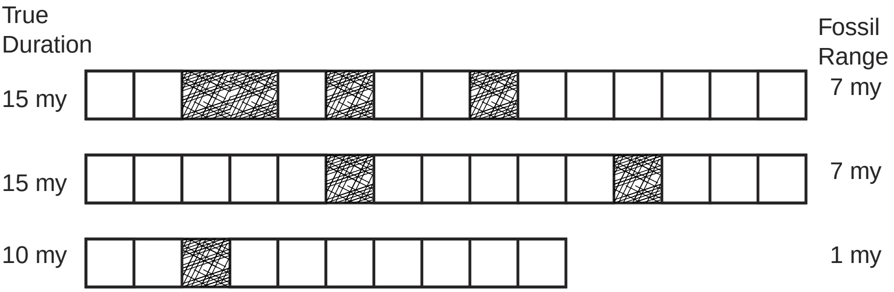

Figure 7.2. Relationship between total life span of a taxon and fossil duration. Time is in discrete bins (1 million years for this example). Empty bins indicate no preservation. (After Foote and Raup 1996.)

Table 7.1. Various Estimates of Preservation Probability and Completeness of the Record of Fossil Taxa

Taxon (Number)	Median Duration (Million Years)	Standard Deviation	Preservation Probability	Standard Deviation	Completeness	Standard Deviation
Trilobite species, Upper Cambrian, Lower Ordovician (101)	0.15	0.05	0.73 per 60-foot interval	0.25	0.9	0.029
Crinoid genera, Ordovician–Devonian (395)	7	0.8	0.5 per stratigraphic interval (mainly series and stages)	0.082	0.7	0.018
Mammal species, Cenozoic of North America	1.7	0.1	0.25 per 7-million-year interval	0.016	0.6	0.007
Bivalve species, Jurassic of Europe	8.0	1.0	0.87 per 5-million-year interval	0.16	0.9	0.012

(From Foote and Raupe 1996, with permission.)

One must remember, however, that this estimate is inevitably on the high side, because it derives from places where fossils are already known to occur. If entire parts of the rock record are missing, owing to erosion, nondeposition, and so on, then many more taxa will fail to be preserved than Foote and Raup's estimates suggest. The results, as encouraging as they are, must also be scaled to the minimum resolution of a geological section. In the case of the trilobites, this is about 18 meters, but it is not clear what this amounts to in absolute time. The median taxon duration was 150,000 years (Stitt 1977), which is encouraging, given that invertebrate fossil ranges are often much longer, but not so encouraging if one wanted to study fine-scale evolutionary dynamics (see chapter 6).

Another way of estimating completeness would be to estimate for a phylum or other higher-level taxon the proportion of living families with a fossil record. As might be expected (Figure 7.3), the range is enormous. For Malacostraca, whose preservation is sporadic at best, the proportion is less than 0.2, but echinoids, bivalves, and brachiopods surpass 0.9 (Foote and Sepkoski 1999). Using a standard timescale, Foote and Sepkoski found that taxon completeness, as defined above, is well correlated with the proportion of living families that are preserved as fossils. Most points are skewed toward the proportion of extant families, suggesting that the Recent has a strong influence on what part of the fossil record is well preserved and perhaps even on our ability to recognize taxa effectively. The brachiopods are surprisingly complete from both measures. The cephalopods run against the trend, but this is probably because there is only one living shelled group.

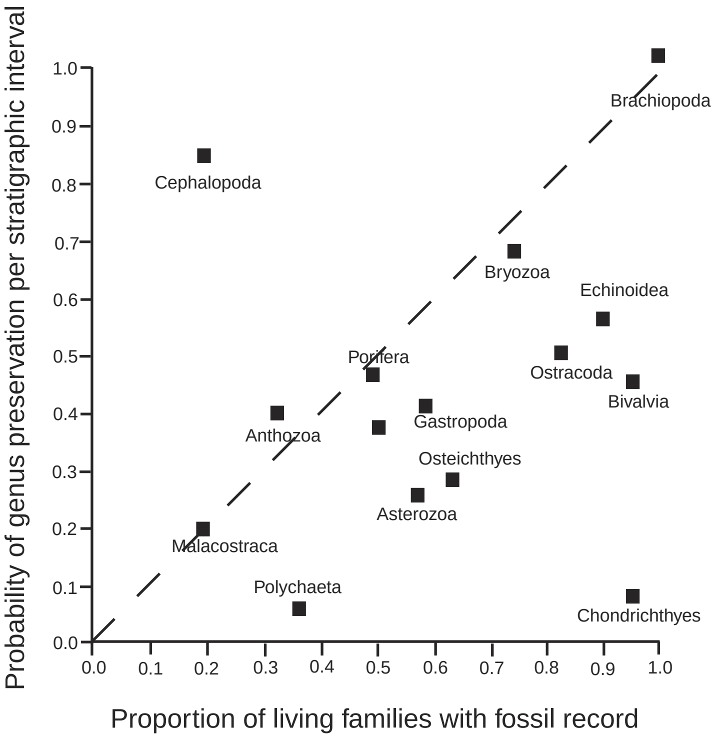

Figure 7.3. The relationship between proportion of living families preserved as fossils and another estimate of completeness of preservation, using one of the data sets analyzed by Foote and Sepkoski (1999).

The Overall Pattern

Diversity. As mentioned above, the concordance of several independently compiled data sets at several taxonomic levels (Sepkoski et al. 1981) lends credence to a general pattern of changing taxon richness throughout the Phanerozoic. The pattern can be conveniently described from Sepkoski's (1984) analysis of the fossil record at the family level. The overall richness curve (Figure 7.4) is divided into three principal times of diversification: (1) Vendian–Early Cambrian interval, with a slowing of diversification in the Middle and Late Cambrian; (2) Ordovician radiation, followed by stabilization between the Late Ordovician and Early Permian; and (3) Mesozoic–Cenozoic expansion. These expansion periods are punctuated by a series of mass extinctions, which we shall discuss below. Sepkoski (1984) argued that the overall pattern is one of three sequential logistic curves; this presumes that the period of Cenozoic expansion is dampening. Sepkoski (1996) portrayed the Paleozoic record of articulate brachiopods as a logistic expansion, but diversity is dampened toward the end of the Paleozoic by the rise of bivalves. The interaction can be modeled by coupled logistic equations, inter-

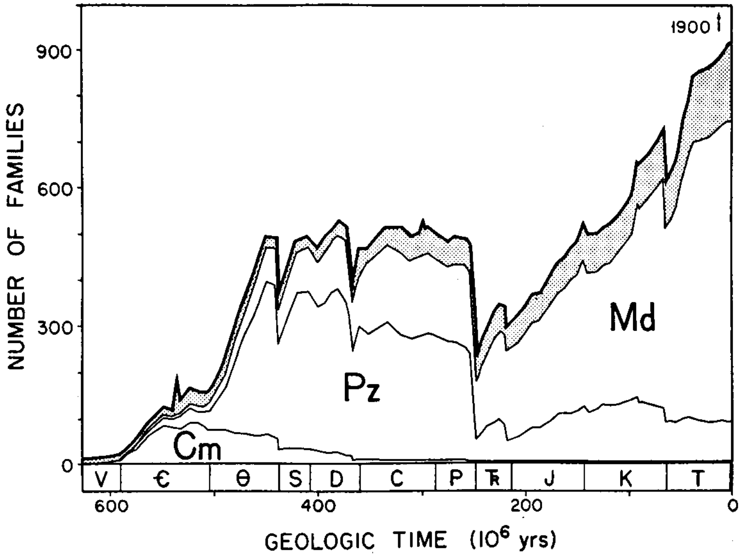

Figure 7.4. Family diversity through the Phanerozoic. Shaded area represents poorly preserved taxa. Three remaining fields comprise the relative contribution of the evolutionary faunas (Cm = Cambrian, Pz = Paleozoic, Md = Modern) to the total diversity of well-skeletonized taxa (see text). The number 1,900 represents the approximate number of extant families. (From Sepkoski 1984, with permission.)

rupted by the Permian extinction. In an analysis of another compilation of stratigraphic range data (Benton 1993), the Phanerozoic record appears to reflect an exponential increase of taxa, punctuated by a few major and relatively sudden extinctions (Benton 1995).

Evolutionary faunas. Both the expansions and extinctions are characterized by coordinated changes of unrelated taxa. This has long been recognized qualitatively, and was quantified by Cloud (1948) with an earlier marine invertebrate data set. He termed the expansions *evolutionary outbursts* or *eruptions*. Bursts within the articulate brachiopods were correlated with periods of expansion of morphological diversity, many of whose taxa were short lived (Cooper and Williams 1952). Many newly appearing groups occur complete with their associated ecological community. As Camp (1952) noted:

> New elements usually appear in the record as migrants from an unknown geographic center. . . . When they appear they may already be accompanied by new complementary elements (i.e., herbivores plus highly developed carnivores); which makes it probable that we seldom see even the approximate time of original appearance of a group.

Darwin was right about gaps in the record.

The more recent statistical studies provide bases for more careful analysis, as they correct for the different time intervals represented by geologic periods and epochs and have the benefit of various taxonomic revisions and later discoveries. Most notable is Sepkoski's (1982, 1993) compendium of fossil marine families, which is constantly being updated.[1]

Although evolutionary expansions are rather clear when analyzed in toto, a closer look reveals geographic differences. Miller (1997) examined rates of diversification of Ordovician brachiopods and found very different patterns of expansion in different geographic provinces. Hoffman (1989b) argued that even mass extinction at the end of the Cretaceous was far different in intensity in different regions. Thus, we may be in for a surprise as to the simultaneous nature of events that we have formerly regarded as global in extent. This does not mean, of course, that the subdivided expansions reported by Miller are not caused by a common global change. But it is equally possible that evolutionary innovations that appear in one basin develop for a long time before chance dispersal brings them to other basins.

Times of biotic change can be detected if we examine *taxon turnover,* a measure of appearances plus extinctions (high turnover can occur when appearances and extinctions are equal), which determines *standing taxon richness,* the number of taxa present at any one time. A decline in standing taxon richness, for example, may result from constant extinction rates with declining speciation rates. Correspondingly, an increase in standing taxon richness may derive from constant speciation rates and declining extinction rates. A mass extinction, therefore, may derive from no increase in extinction rates, although in reality this always happens.

Using a *Q*-mode factor analysis of occurrences of marine and terrestrial families through the Phanerozoic, the pioneering study of Flessa and Imbrie (1973) measured the coordination of diversity change among family-level taxa. This analysis establishes a series of composites that behave statistically independently. Distinct associations dominated successively through geological time. Ten marine factors explained 96% of the fluctuations of diversity, whereas four terrestrial diversity associations explained 91% of the data. Taxonomic turnover (extinctions plus appearances) of the marine and terrestrial assemblages showed distinct peaks, as was found earlier by Newell (1952); neither the associations of taxa nor their temporal disposition could be reckoned with a random distribution. The temporal pattern of first appearances of families was also in most cases nonrandom (Flessa and Levinton 1975).

The establishment of statistically independent associations by factor analysis does not guarantee any biological significance. Further supportive evidence would be required to establish whether a given assemblage consisted of either an interacting and interdependent group of species or a group of species that responded similarly to the same environmental changes. At present, we have no such evidence for interdependence.

Flessa and Imbrie (1973) also devised a measure of turnover based on the angular change between assemblages that are each expressed as a vector among the factor axes. The peaks in turnover corresponded weakly to tectonic events. They

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[1] Jack Sepkoski died in 1999. We lost a superb scientist and a kind soul.

argued that the turnover peaks may be related to biogeographic readjustments, due to rearrangement of dispersal routes and change of climate accompanying continental movements. They found no obvious correlation with area of continental inundation. Thus, though some conspicuous extinctions are correlated with sea-level fall (Hallam 1983), a general explanation may have to involve several different factors in turnover and extinction. An analysis of turnover and extinction in Neogene planktonic Foraminifera (Wei and Kennett 1983) showed a strong correlation with changes in Cenozoic world climate

Sepkoski (1984) performed factor analysis and recognized three distinctive major *evolutionary faunas* (EFs), which are not too different from those of Flessa and Imbrie. The *Cambrian EF* (Figure 7.4) is dominated by trilobites and inarticulate brachiopods, expands during the Cambrian, and reaches a plateau in the Middle Cambrian, followed by a long, slow decline through the Paleozoic. The *Paleozoic EF,* dominated by articulate brachiopods and other classes, appears at the same time as the Cambrian EF but radiates more slowly until the end of the Cambrian, when a rapid diversification ensues in the Ordovician. After a plateau, a long decline occurs from the end of the Middle Devonian to the end of the Paleozoic, when the Permian mass extinction decimates it. Finally, the mollusk-dominated *Modern EF* appears in the Early Cambrian, then expands even more slowly than the Paleozoic EF and increases as the Paleozoic EF is decreasing, so that it is approximately 40% of the total diversity just prior to the Permian extinction. Because the Modern EF suffered less in the Permian extinction, it came to dominate Triassic faunas and has been expanding ever since (Sepkoski 1984). An interesting detail is the higher expansion rate of the Paleozoic EF in the Triassic, after the Permian extinction, repeating its higher capacity for expansion than the Modern EF in the early Paleozoic. Its ultimate failure seems due more to its relative sensitivity to extinction than to a failure to diversify.

As mentioned above, the objective of documenting changes in fossil species richness often depends on the assumption of a linear relationship between number of higher taxa and number of component species. A comparison of temporal changes at the phylum, ordinal, and family levels (Figures 7.4 through 7.6) illustrates that something more than overall species richness is being documented. The number of phyla stabilized in the Ordovician and has not changed since. The number of orders stabilized by the mid-Paleozoic. In contrast, the number of families has had a far more volatile history, but overall trends are probably qualitatively concordant with the number of species.

This hierarchical response pattern, first noted by Valentine (1968), suggests that differing mechanisms may be operating at the various levels. If the phylum level represents fundamental morphological differences, most major divergence had ceased to occur by the beginning of the Ordovician. The ordinal-level diversity ceases to expand soon thereafter, but here there is extensive turnover. Stability in numbers of order-level taxa means something different than at the phylum level. Despite a major period of evolutionary expansion in the Mesozoic and the occurrence of major ecological changes in the Mesozoic marine benthos (Thayer 1983; Vermeij 1983), no new phylum-level morphological innovations occurred, and the

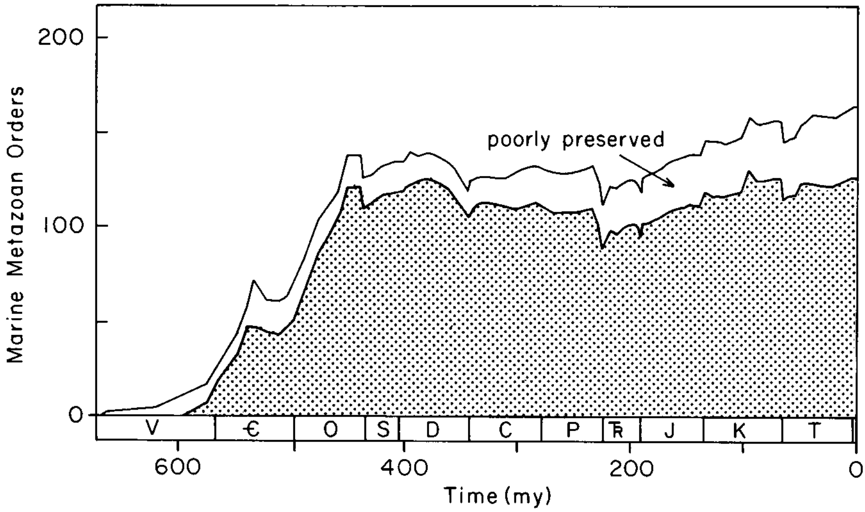

Figure 7.5. The Phanerozoic record of diversity of marine metazoan orders. (After Sepkoski 1978.)

standing diversity of morphological variation (ordinal-level diversity) has not expanded since the Ordovician. The Silurian animal conquest of land must have been a major event in physiological evolution, but no exclusively terrestrial animal phyla are recognized. Ecological pressure may have induced adaptive morphological change, which seems to have been limited after the Ordovician. This is one of the fossil record's most important and enigmatic messages. Apparently, evolution has had to work with that phylum-level diversity that existed by mid-Paleozoic. All subsequent evolution seems to have been constrained by this initial pattern of dominance.

If we examine the Vendian and Early Cambrian periods of expansion, the impression of extensive morphological innovation is only increased. A widespread Late Precambrian fauna, whose representatives were first described extensively at Ediacara, Australia (see Glaessner 1984 and references therein), consist of a wide spectrum of organisms with no obvious modern relatives. It may have been an early evolutionary expansion that failed. These were exclusively soft-bodied forms whose generally poor preservation precludes any certainty of their extinction before the beginning of the Cambrian. Even in the Cambrian, a wide variety of groups exists, with occasional obvious phylum affinities but no clear association with living classes or orders.

The upswing: Why? Everything we have learned about the fossil record reveals beginnings: the Cambrian–Ordovician radiation; a series of Precambrian radiations; the Cenozoic radiation of mammals, insects, flowering plants, and many other groups. But why? The first thing that comes to mind is the notion of a vacuum. Either the environment was "empty" to begin with (the Cambrian radiation?) or was emptied by a global catastrophe, to be later filled in by founders of a new radi-

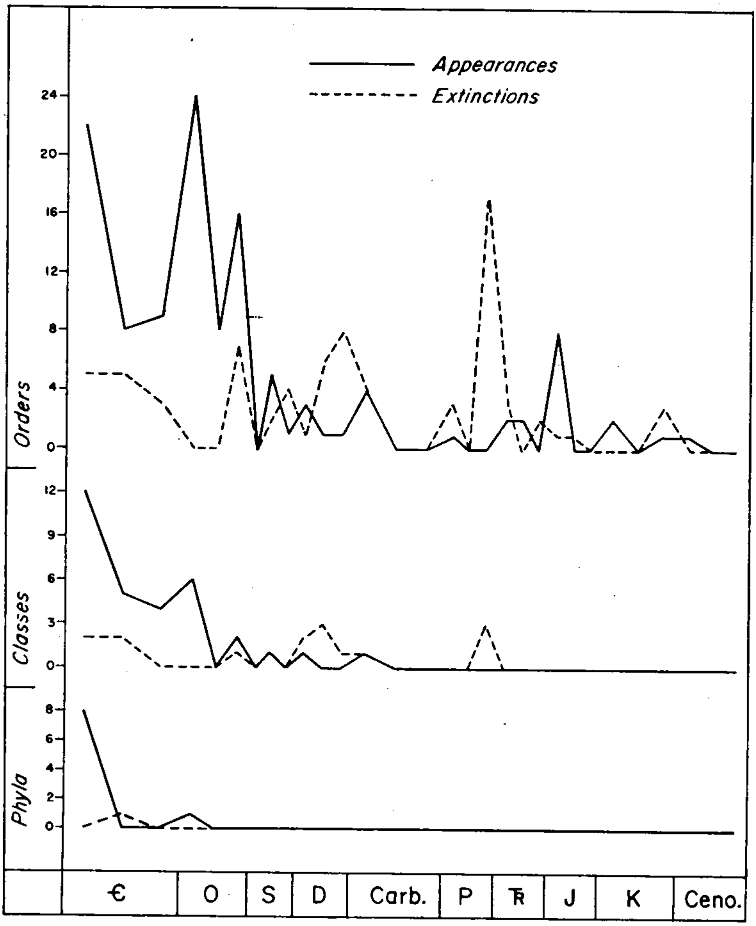

Figure 7.6. Appearances and extinctions of phyla, classes, and orders of continental shelf benthos. (From Valentine 1969, with permission.)

ation (the Permian–Triassic episode?). It is difficult to define what we mean by *empty* in the first place. After the dinosaurs became extinct, was there a void during the Paleocene? There were no huge herbivores, no gigantic carnivores, no gigantic ammonites to feed on the ocean's animal prey. One senses that there was an opportunity, but the modern orders of mammals did not burst onto the scene until nearly 10 million years later, after the end of the Paleocene.

We are comfortable with a research agenda for studying large-scale extinctions. We simply look for catastrophic environmental changes (see below). But what do we look for to study beginnings? We can imagine a few components that might have caused evolutionary radiations:

1. Vacuum, plus environmental change that stimulates a radiation
2. Extinction of a competitor, allowing a surviving group to radiate in its place
3. Both are required in combination

The Cambrian radiation, discussed in the next chapter, might be an example of the vacuum hypothesis. Perhaps an increase of oxygen or an amelioration of climate allowed the newly established vacuum to be filled. It seems reasonable to assert that there were no opportunities for a diverse array of large-bodied animals to exist much before the Cambrian. But why the radiation happened in the Lower Cambrian and not earlier might be reasonably explained by some environmental shift. It is also possible that some biological interaction with an as-yet unknown Precambrian denizen inhibited the rise of animals.

Later on in the geological record, things are even less clear. As we discuss below, it does seem that radiations do not occur during the decline of predecessor groups; that is, new radiations typically did not drive older groups to extinction. But were the new radiations merely inevitably filling a vacuum created by the previous extinction? This is not very clear as yet, especially because there is an inevitable delay in reradiation following an extinction (see below), and it is not clear whether this is a period of continued environmental stress or just represents a lag time that cannot be filled by a new radiation immediately. If the latter were so, we would have to wonder about the Cambrian radiation, which supposedly occurred in as little as 10 million years (see chapter 8). Why did it take about 10 million years for the modern orders of mammals to appear after the Cretaceous mass extinction?

The end of the Paleocene was marked by a major paleooceanographic event (Kennett and Stott 1991). A major extinction wiped out much of the benthic foraminiferal biota, although plankton was left more or less intact. Deeper water was likely warmer and dysaerobic, which hastened the extinctions. The warming temperature might have caused a major geochemical change as well. Decomposition of methane hydrate in the sediments might have resulted in a release of methane and carbon dioxide, which eventually influenced both marine and atmospheric warming (Kaiho et al. 1996). A sudden decrease of $^{13}C/^{12}C$ ratios occurred both in the terrestrial and marine environments, suggesting a large-scale increase in temperature. Koch, Zachos, and P. D. Gingerich (1992) argued that this climate change might have stimulated the radiation of the modern orders of mammals. A worldwide amelioration of climate might have permitted the rise of new groups in a restricted area to spread throughout the world, displacing more archaic groups of mammals.

This scenario, if true, would suggest that it is not enough to have a vacuum created by a previous extinction. The opportunity for a new radiation may require appropriate conditions, perhaps a threshold size of geographic area for opportunity to be translated into dispersal and evolutionary radiation.

Taxon Longevity and Lyellian Curves

As discussed in chapter 6, taxonomic longevity is used commonly by paleontologists to estimate the tempo of evolution within a clade. Longevity estimates have also been used to contrast groups with differing ecology and taxonomy. The longevities of taxa vary extensively, although there is considerable uncertainty in any one estimate. A common problem is distinguishing between *pseudoextinction,* in which one species evolves directly into another simply by evolving a new morphology anagenically, and true extinction, when a taxon dies off. Table 7.2 shows some estimates for various fossil groups.

The frequency spectrum of longevities at a given taxonomic level within a more inclusive taxon has also been used in various models of evolution (Levinton and Ginzburg 1984; Van Valen 1973b). Longevity can be catalogued directly from the first and last occurrences of the group in question. Sporadic occurrence often makes it necessary to assume that these occurrences are not just a small part of the total duration. Estimates of longevity are biased by the minimum stratigraphic time resolution.

The disappearance of given taxa with increasing time from either the present or a given stratigraphic level, the *reference time datum* (RTD), can estimate mean longevity (Figure 7.7). In the case of extant taxa, such an approach is essential, as we do not have a complete record of the future longevity and therefore have no extinction point. In the case of fossil taxa, it is sometimes more reliable to examine the overall pattern of disappearance of a group of taxa from one 'RTD' backward than to tabulate individual durations, which are subject to many sorts of collecting bias. The gradual disappearance of an entire fauna when sampled backward in time may give a smooth loss curve, as first discovered by Lyell in his investigation of mollusks. Stanley (1979) therefore coined the term *Lyellian curves* for plots of loss of taxa before the present. *True Lyellian curves* plot the percent of a fossil fauna that is still extant. Although there is increased error (as Stanley 1986a noted), it is also possible, however, to simply plot the fractional loss of the extant species as a function of time before the present, or any other RTD.

Table 7.2. Estimates of Species Longevity for Various Fossil Groups

Taxon	Species Average Lifespan (Million Years)
All invertebrates	11
Marine invertebrates	5–10
Marine animals	4
Marine animals	5
All fossil groups	0.5–5
Mammals	1
Cenozoic mammals	1–2
Diatoms	8
Dinoflagellates	13
Planktonic foraminifera	7
Cenozoic bivalves	10
Echinoderms	6
Silurian graptolites	2

After May et al. 1995, and references therein.

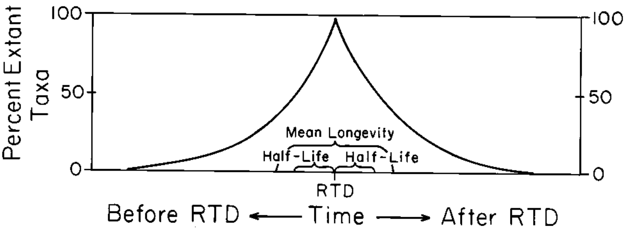

Figure 7.7. Simple model of loss of extant species, before or after a reference time datum (RTD) in the fossil record. Assuming a constant rate of loss, half-life and longevity are indicated.

In true Lyellian curves, one must assume that the overall diversity has remained constant in order to estimate longevity. Lyell held to a concept of plenitude and believed that as one species became extinct, it was immediately replaced. If diversity rapidly increases toward the Recent, for example, the loss of living taxa as one samples back in time will give an underestimate of longevity, as a disproportionate number would have arisen recently. Similarly, if a recent extinction event had occurred, going back in time will yield a sudden abundance of those taxa that became extinct; this, too, will give an underestimate of true longevity. It is therefore better to tabulate the presence of species and plot a *cohort loss curve* of percent of taxa present at an RTD, with increasing time before or after the RTD (see Raup 1978). To obtain an estimate of mean longevity, some model of loss is assumed, such as a constancy analogous to radioactive decay. This analysis is to be distinguished from so-called *taxonomic survivorship curves.*

Assuming that the extinction for a given group occurs at a given rate, the rate of change in the number of taxa, N, disappearing with time before the RTD should be proportional to a rate constant, k (Kurtén 1959a).

$$dN/dt = -kN$$

The change in taxonomic richness with time before the RTD is

$$N_t = N_0 e^{-kt}$$

The half-life is therefore the time period over which N_0 decreases to $N_0/N_t = 0.5$. Rearranging and taking the logarithms, where the number of taxa has decreased to $0.5N_0$, gives

$$T_{1/2} = 0.693/k$$

But k is proportional to the reciprocal of longevity, T. Therefore, longevity is proportional to $1.443T_{1/2}$. To get the true value of T, we must double this, as our derivation applies only to the portion of the life span of a taxon before the RTD, which must be symmetrical to the probability of longevity afterward. Therefore:

$$T = 2.886T_{1/2}$$

With pseudoextinction, a Lyellian analysis inflates the true value of T.

When working above the species level, complications arise, as the taxonomic unit of survival consists of component species that have a given rate of appearance and loss (Raup 1978). Thus, the disappearance of a species may not result in the loss of the taxon at a higher level (e.g., family). Furthermore, a speciation event may result either in a member of the same higher taxon or in a new taxon, especially given the use of phenetic criteria in defining the latter. Raup used a random branching model to determine species longevity from generic longevity. If cohorts of genera are employed, a smoother loss can be seen in the readily preservable marine benthic groups, with increasing time from a series of RTDs, corresponding to the beginning of the various Phanerozoic periods. A mean species duration of 11.1 million years arises from this analysis, which is somewhat greater than other estimates. The mean is far greater than some groups, most notably ammonoids (1.2 to 2 million years), graptolites (1.9 million years), and Cenozoic mammals (0.7 to 1.4 million years).

Stanley (1975, 1979) applied an ingenious technique to estimate speciation rate, and longevity. Assuming that speciation is constant, the number of extant species and the time of origin may be used to estimate a rate of splitting (he assumed dichotomous splitting). This approach can work only if the group is still actively undergoing cladogenesis, with a net constant rate of species increase. For bivalve mollusks, the number of species of extant families is linearly related to the logarithm of time of origin. Unfortunately, the technique has limited value, as it is questionable whether most groups have a constant splitting rate over periods long enough to get a reliable estimate. Wilson (1983) analyzed the Coleoptera, Diptera, and Hymenoptera and failed to find any such relationship. Nevertheless, the quite different longevities are similar to those reported by Stanley. It seems unlikely that any overall biases in the data will contribute to making average mammalian species longevity much greater than that of bivalve mollusks, for example.

To justify a natural order among different taxonomic groups, it would be necessary to demonstrate, within a taxon, a degree of homogeneity of species longevity over time, in comparison to overall differences with other groups. At present, the available data are too scattered to give anything other than a vague impression. *Iterative evolution,* or repeated radiations following extinctions, is common enough in fossil groups to provide an opportunity to compare longevity. Cifelli (1969) described the two evolutionary radiations of planktonic Foraminifera during the Cenozoic. Globigerinoid ancestors in the earliest Paleogene gave rise to a morphologically diverse clade that decreased in diversity toward the end of the Oligocene. Subsequently, another radiation in the Neogene reproduced nearly the same spectrum of morphologies. A compilation of Caribbean species longevities (Levinton and Ginzburg 1984) permits an evaluation of the quantitative aspects of the two radiations. Figure 7.8 shows the distribution of longevities for the Paleogene (N = 128) and Neogene (N = 59) radiations. They point to a remarkable similarity of modal longevity and distribu-

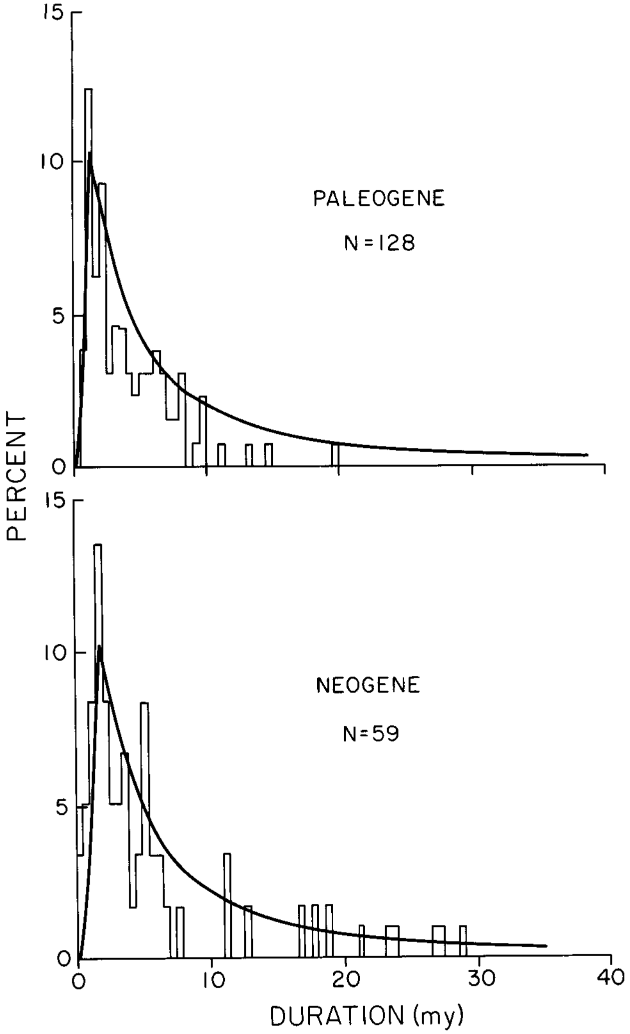

Figure 7.8. Distribution of longevities for Paleogene and Neogene species of Caribbean planktonic Foraminifera. Model of random appearance and extinction is shown for comparison. (After Levinton and Ginzburg 1984.)

tional shape (Paleogene median longevity = 3.40 million years; modal longevity = 1.5 million years; Neogene median longevity = 3.62 million years; modal longevity = 2 million years for extinct taxa). Using a logarithmic correction to achieve normality, the mean of the two distributions does not differ significantly (Student's t test, $p > .05$). A Kolmogorov–Smirnov test on the cumulative distribution, however, shows a significant difference ($p < .01$). The latter test is far more sensitive to differences of small magnitude, with large sample sizes.

Some studies of longevity suggest significant temporal variation. Stanley (1979) estimated mean bivalve species longevity to be 11 million years. This is far greater than the estimate of about 1 million years for Cenozoic mammals. But in some periods, mean species longevity of bivalves deviated significantly from the overall value. In the Cretaceous of the western interior of the United States, the mean species duration for the *Sciponoceras gracile* zone is 1.82 million years, with a duration over several ecological groups of 1.82 to 2.20 million years (Koch 1980). Kauffman (1978) found similarly brief longevities in the Upper Cretaceous. Mammalian species longevity has also varied substantially (Kurtén 1959b). Paleocene (1.5 million years) and Pleistocene (0.6 million years) values are low, but Neogene values are 5.2 million years, well within the range of bivalves.

Taxonomic survivorship. The longevities of a group of extinct fossil taxa can be compiled into a *taxonomic survivorship curve,* which treats the group as if it were a cohort and records the cumulative loss as a function of increasing longevity. In a semilogarithmic plot, the magnitude of the slope gives the mean longevity, and the departure from linearity is a measure of the probability of taxon survival with increasing age. Thus, a linear slope indicates that the probability of survival is independent of age, and mean age corresponds to probability of extinction for the species. Linearity would imply that some process sets the mean extinction, but variation around the mean is a random process. Van Valen (1973b) formulated a unit, the macarthur (ma), which corresponds to a taxon survival rate giving a half-life of 500 years. Note that this survivorship curve and half-life are different from Lyellian and cohort survivorship curves, which truly measure loss of taxa from a given time. As in the case of Lyellian curves, the slope yields a measure of mean longevity, so differences in slope among major taxa might indicate differences in overall biology (Levinton 1974; McCune 1982).

Some biases occur in taxonomic survivorship curves, but they have not been analyzed in most studies. At higher taxonomic levels, complications arise as species are both appearing and disappearing within the same taxon. Survivorship curves constructed from such composites should be concave up, rather than linear, if the probability of species-level extinction is constant and independent of taxon age (Holman 1983; see also Raup 1978). The slope of family-level survivorship should be shallower than or equal to that for genera. The number of species per genus is a factor in survivorship at the supraspecific level, rather than the variation in longevity of component species (Arnold 1982). The survival of a genus may simply be proportional to the number of component species.

A bias also stems from the minimum resolvable time units that are employed (usually geological stages) to measure longevity. If a taxon is found in one stage, its longevity is, by definition, a function of the time represented by that stage. Because stage time lengths are roughly lognormally distributed, a mildly concave curve can be made to look linear from the time bias. A taxon straddling two unusually long stages would appear to have a greater longevity than another straddling two short stages (Sepkoski 1975). The average length of stages differs throughout geological time (Flessa and Levinton 1975). This effect can make taxa confined to one set of stages appear to differ in longevity from another set. Also, the minimum length of time resolution must also produce a flat top near the beginning of the survivorship curve (Raup 1975).

Van Valen (1973b) used a large compilation of different groups, at various taxonomic levels, to show that taxonomic survivorship curves appear to be linear. A statistical test for linear decay showed that the survivorship of the ammonoids is linear, if one subtracts the initial flat top due to the bias of minimum time resolution (Raup 1975). But many of the other cases are ambiguous. Levinton (1974) examined survivorship curves for suspension-feeding and deposit-feeding bivalve molluscan genera and found a strong linearity, except for small sets of genera that were geographically widespread and tended to exist over the same long spans of time. These superposed a ledge on the otherwise linear curve. Suspension feeders had a lower rate of survival, which might be related to their relatively volatile response to changes in food in the water column. Arnold (1982) examined species-level survivorship in the Cenozoic globigerinoid Foraminifera and also found linearity.

Survivorship curves sum up the longevity spectrum of a group over its entire duration, which may obfuscate a temporal pattern of changes in taxon longevity. For example, taxon longevity may be low and then high. When summed into a survivorship curve, this might yield a cumulative distribution producing a straight-line survivorship. In the development of a Cambrian biomere – a probable radiation initiated by an onshore arrival of taxa – taxon longevity is at first quite short, then longer, then short again (Hardy 1985; Stitt 1971). The summed longevity curve would thus be misleading because it might give the false impression of some probability distribution of mortality as a function of age that is independent of time.

Stochastic Models of Appearance and Taxon Longevity

Are appearance and extinction a matter of chance? The temporal trends and stable phases of taxon richness occur with extensive turnover at the family level. Most paleontologists have reckoned the extensive changes in the fossil record as products of forces in the environment (e.g., Flessa and Imbrie 1973; Newell 1952; Valentine 1971a, 1971b). Raup, Gould, Schopf, and Simberloff (1973), however, raised the intriguing possibility that the overall temporal pattern might be explained by stochastic appearance and extinction. They performed a series of simulations assuming equal probabilities of appearance and extinction, with an upper limit on species richness. The results looked superficially like the many "spindle" diagrams of temporal changes in diversity so common in paleontological publications.

Gould, Raup, Sepkoski, Schopf, and Simberloff (1977) used the simulations to measure shapes of clades and defined the temporal position of half of the area of a spindle diagram as the *center of gravity.* Simulations based on a stochastic model produced a mean center of gravity of about 0.5. This was similar to theirs and Sloss's (1950) analyses of many real clades, with the exception of those in the middle of a major radiation, which are bottom heavy (center of gravity < 0.5). Stanley, Signor, Lidgard, and Karr (1981) argued that any stochastic branching process with equal probabilities of appearance and extinction would not permit large expansions with any acceptable level of probability. Sloss (1950) also suggested that clades probably were initiated by some process that accelerated cladogenesis.

Though the shape of clades may reflect a random process, the timing of appearance and extinction is usually far from random. The very presence of evolutionary faunas deducible by factor analysis (Sepkoski 1984) suggests that coordinated evolution occurs among unrelated groups. Flessa and Levinton (1975) analyzed first appearance in a wide range of fossil groups and found that unlike the simulations of Raup et al. (1973), real appearances were aggregated in time. Gilinsky and Bambach (1986) reached similar conclusions when considering diversity changes during the history of a clade. It is therefore untenable to consider the entire historical picture as reflective of a stochastic process; but this does not preclude such an explanation for parts of the overall pattern.

Can longevity be explained by a random model? Van Valen (1973b) suggested that challenges sufficient to drive a species to extinction might appear continuously. He used the Red Queen's dictum – you have to keep on moving to stay in the same place – as a metaphor to describe the continuous set of biological challenges presented to a species. It is also possible that species longevity is completely random, with mean longevity controlled by some characteristics of the biology of the taxon independent of other species. Ginzburg (Levinton and Ginzburg 1984) devised a stochastic model that predicts the distribution of taxonomic longevities by estimating the time over which a population with a zero average growth trend fluctuates before extinction. Consider a population growing exponentially with a stochastically varying growth rate:

$$dN/dt = [\mathrm{r} + \sigma\varepsilon\{t\}]N$$

where N is the population size, t is time, r is rate, σ is the standard deviation of the growth rate, and $\varepsilon\{t\}$ is the standard normal white-noise process [mean $\varepsilon = 0$; variance $\varepsilon = 1$]. For the initial population size N_0 and the critical level $N_c < N_0$, the probability density of the first passage of the process N_t through the critical level N_c shows that an increase in the variance of the population growth rate decreases the probability of surpassing the threshold for persistence, whereas increased r raises the probability. Therefore, taxa with large variance relative to mean growth rate will most likely go extinct rapidly, whereas those taxa with high r or large population size, relative to the threshold, will tend to persist.

Over the long run, it is reasonable to assume that $r = 0$ – that is, no long-term positive or negative growth trend owing to deterministic forces. One then can compute the passage time from birth to extinction. The typical appearance–extinction process with $r = 0$ should look like the diagram illustrated in Figure 7.9. Here, N_r is the threshold of abundance above which one recognizes the taxon in the fossil record, t_A is the time of first appearance, t_{-RA} is the time of recognized appearance, t_{RE} is the time of the recognized extinction, and t_E is the actual time of extinction. The observed longevity, which is the total duration over which it is possible to col-

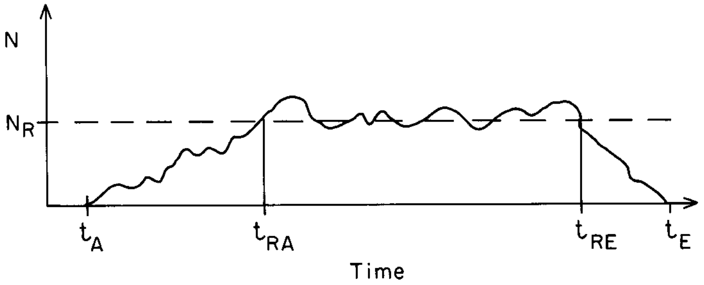

Figure 7.9. Stochastic model of the appearance and extinction of a fossil taxon, relative to a recognition threshold (see text for explanation). (After Levinton and Ginzburg 1984.)

lect the taxon as fossils, $t_{RE} - t_{RA}$, is the time between the first and last passage of the stochastic trajectory through the recognition level. Period $t_E - t_{RE}$ is much shorter than period $t_{RE} - t_{RA}$.

The first passage time model can be fitted to actual frequency distributions by taking the modal longevity, t_m, from the data, and calculating the probability density of extinction (cf. Levinton and Ginzburg 1984). Figure 7.8 shows that the overall fit is good in both Paleogene and Neogene radiations, though there is a significant excess predicted for the right tail of the distribution and a deficiency at the modal longevity relative to the actual data. Using a one-sample G-test, the difference with the model is significant (first radiation: $G = 102.4$, 39 *df*, $p < .001$; second radiation: $G = 56.7$, 39 *df*, $p < .001$).

The reason for a significant difference between the model's prediction and the actual data may be due to at least three possible sources of empirical and theoretical error. First, some long-lived taxa may be artificially absent. If taxa are defined by pseudoextinction, then a long-lived single taxon may appear in the data as a chain of morphologically transitional shorter-lived taxa. Phyletic evolution from one morphologically defined species to another is common in planktonic Foraminifera (Kennett and Srinivasan 1983). Second, r, the intrinsic rate of population increase, is assumed to be zero. If r does not equal zero, then the variance of r would be an important component of stochastic extinction, and, hence, taxonomic longevity. If r does not equal zero, we can improve the model's fit to the data. As we have no basis to select the value of parameters, such an attempt at this stage would constitute mere curve fitting. Finally, of course, the model may be incorrect. The relatively kurtotic aspect of the real data, combined with a deficiency of long-lived forms, may suggest that some nonrandom process narrows the longevity spectrum.

Regulation of Diversity

The pattern: A series of steady states? On the grand scale, it seems absurd to believe that a steady state has been developing, especially given the obvious explosive rise in families, genera, and species through the Cenozoic. Nevertheless, there are interesting cases of constancy of diversity over time at many taxonomic levels. Sepkoski's (1984) analysis of family-level taxon richness demonstrated some apparent long-term periods of relative constancy. One can also see such stability in terrestrial faunas. In the mammals, after a Paleocene–Eocene radiation and an Oligocene decline, long-term stability in the number of families prevailed (Figure 7.10), despite extensive turnover (Lillegraven 1972). Such stability can also be detected at the species level within communities. Boucot (1975, pp. 226–237) documented a similarity in species richness over a 100-million-year span in Silurian–Devonian brachiopod communities despite extensive phyletic evolution and cladogenesis. Boucot (1978) documented many other such examples, which he termed *ecological-evolutionary units*, or EEUs. The fossilizable component of very nearshore marine benthic communities had essentially the same species richness throughout most of Phanerozoic time, as opposed to the changing offshore environment (Bambach 1977). Wei and Kennett (1983) recorded a period of stability of 10 million years for Neogene planktonic Foraminifera, following an early diversification. Of particular interest is a detailed study of a deepening Late Ordovician nearshore assemblage, where a maximum species richness was achieved rapidly and maintained for 3.5 million years, despite about 15% turnover per 1 million years (Bretsky and Bretsky 1976; Rosenzweig and Duek 1979). Over the period of stability, half the steady-state diversity turned over. Bretsky and Bretsky found a steep relationship between standing diversity of benthic invertebrate species and number going extinct from one stratigraphic level to the next, but only a shallow relationship of appearances to standing diversity. This suggests that extinction is the major factor in maintaining the steady state. During the colonization period, species persistence within the area was less than after the steady state was established; this may suggest something about the instability of the early habitat as it was colonized, or perhaps something about the competitive success of the later species (Rosenzweig and Taylor 1980). Persistence is not nec-

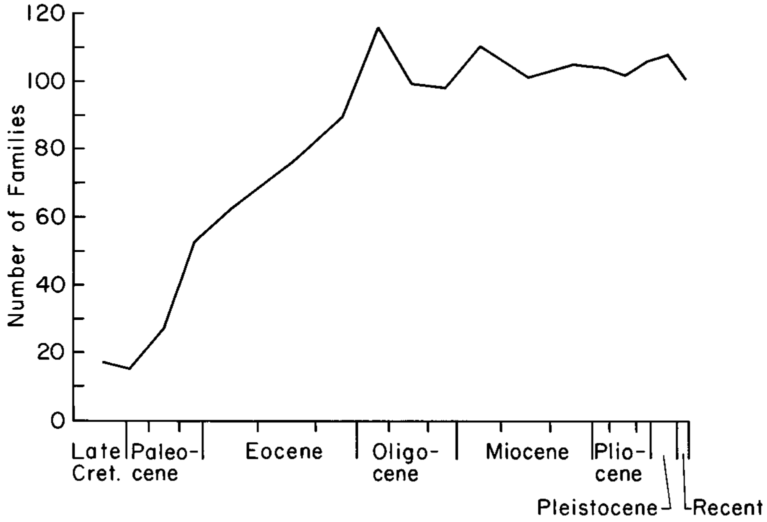

Figure 7.10. Number of families of mammals from the Late Cretaceous onward. (After Lillegraven 1972.)

essarily equal to longevity, as there is no evidence that many of the species were endemic. Hoffman (1985) analyzed global patterns of diversity and found no general correlation between taxon richness and extinction rate. But the smaller-scale studies commonly show temporal constancy in taxon richness. There must have been diversity-dependent effects, as a stochastic process would lead to drift from constant taxon richness levels.

Sepkoski (1978) employed a logistic model to characterize the temporal increase in taxon richness toward a steady state. Sepkoski (1984) used a "three phase kinetic model," employing different divergence rates and limiting values for steady-state diversity for the three evolutionary faunas. When this model was coupled with corrections for mass extinctions, a rather good fit to the Phanerozoic temporal pattern was achieved. The Mesozoic and Cenozoic expansion shows only a hint of leveling toward a plateau. Sepkoski claimed that the trend may be leveling off, however, and predicted a steady state some tens of millions of years in the future – a fairly safe prediction!

Using a difference equation approach, Kitchell and Carr (1985) questioned several of Sepkoski's conclusions. They employed a model that incorporates the negative feedback of high diversity but uses discrete intervals, as opposed to the continuous feedback that would be present in the differential logistic equation. They find that the apparent plateaus are due more to the effects of mass extinctions, which seem to forestall the ascendancy of one EF over another. Even the large-scale Permian extinction seemed only to delay the ascendancy of the Modern EF. This is an important point, as some others have suggested that the Permian extinction "reset" the biosphere, and a new evolutionary era commenced (e.g., Van Valen 1984). Their results also suggest that an equilibrium between diversification and extinction was never reached, even if those balancing forces were continuously at work. Finally, their study demonstrates that the three EFs are interactive. A model assuming independent diversification and extinction among the EFs cannot account for the successive rises and falls of the three EFs. Kitchell and Carr (1985) confirmed Sepkoski's conclusion that the Cambrian EF had a much greater expansion rate than the other two. The lower expansion rate of the Modern EF and a less dramatic negative feedback may explain its slow ascendancy and lower family-level extinction rate.

Explanations for a steady-state level of diversity. Two alternative models may explain the steady state: the (1) *competitive niche subdivision model* (Rosenzweig 1975; Rosenzweig and Taylor 1980), and the (2) *stochastic area effect model* (Levinton 1979).

The competitive niche subdivision model presumes a frequency dependence between the rate of speciation and the presence of species in an ecologically saturated and environmentally complex habitat. If one species becomes extinct, then another can be expected to fill its place. The structure of the habitat therefore determines the maximum number of species that can coexist, whereas the number of species present is inversely proportional to the speciation rate. Rosenzweig (1978) suggested a model of competitive speciation that is compatible with this scenario. Possible supportive evidence for this model is the convergent structure of geographically separated but ecologically similar living communities (see Cody 1974; Crowder 1980; Fuentes 1976) and the long-term persistence of similar niche structures in some fossil communities (Boucot 1978; Levinton and Bambach 1975; Walker and Laporte 1970). One problem is that most such studies report the presence of species adapted to similar regimes (e.g., a burrower, a tube dweller) in two or more communities widely separated in time. This proves not that the community was saturated but only that convergence has occurred with adaptation of species to similar habitats.

The stochastic area effect model (Levinton 1979) presumes that the overall environment is limiting with respect to resources and that the number of species, therefore, must be in some way related to the number of individuals or the area covered per species. Second, speciation rate is presumed to be a stochastic event that occurs at a certain constant rate, depending on a group's particular biology (Stanley 1975, but see problems above). Finally, extinction is a function both of population size and of area covered. Species with small population sizes and narrow geographic range therefore have a higher probability of extinction. Consider a species newly introduced into this region. If it succeeds in colonizing the whole region, up to carrying capacity, then its chance for extinction, owing to area-restricted catastrophes, would be quite low. Geographic speciation would occur, the number of species would increase, and the average geographic range occupied would therefore decrease. Eventually, the average geographic range would decrease to the point of equilibrium, where extinction by regional catastrophes would balance the introduction of new species. A similar argument applies to the temporal change in population size. Although this is an equilibrium process, rapid shifts in the frequency of local catastrophes, or the speciation rate, would produce concomitant changes in the predicted equilibrium species number.

The stochastic area effect model can explain regional differences in steady-state diversity as follows. The size and nature of local habitat disruptions are larger in some locales. In such cases, the average area occupied by a species must be larger or it will soon be extinct. Differences among habitats in steady state diversity would therefore be due to differences in extinction. Järvinen (1979) found that eastern European bird species' turnover increased with increasing latitude. This is presumably related to the higher frequency of severe climatic fluctuations sufficient to cause local population extinction. This is compatible with Bretsky and Bretsky's (1976) result that the maintenance of the Ordovician steady state was mainly due to extinction. It is also compatible with conclusions from analyses of fossil communities (e.g., Bretsky 1969; Bambach 1977) that nearshore habitats, where extinction rates are likely to be great owing to sea-level fluctuations (see Schopf 1974), have been consistently of lower species richness than offshore habitats. The stochastic area effect model also provides an explanation for the relationship between continental or marine shelf area and number of species (Schopf 1974). Larger areas permit the accumulation of larger numbers of species over time. Assuming that the areal scale of catastrophes is the same in large and small marine basins, the model would predict a greater buildup of taxon richness in large basins than in small basins. Other factors, such as temperature and salinity fluctuations, are liable to be more extreme in shallower waters and in smaller basins.

Because they live in environments of lower environmental variability (at least with regard to physiological variables), offshore species would be expected to have lower extinction rates. (e.g., Bretsky 1969). This may be so, but high offshore marine shelf extinction rates are largely explained by the predominance of groups with high characteristic extinction rates (e.g., articulate brachiopods). In contrast, some groups (e.g., bivalve mollusks) with low characteristic extinction rates are concentrated in nearshore habitats. Within such groups, generic extinction rates are actually higher onshore, as might be predicted from the expectation that nearshore habitats are disturbed more frequently (Sepkoski 1987).

It would be very hard to obtain data from the Recent that are relevant to large-scale disturbances that would test Levinton's model. Small-scale disturbances, such as single tree falls, are irrelevant. As might be expected, such small disturbances often exert no strong effect on diversity, because surrounding individuals – members of the dominant species – might soon grow in to fill the patch. In rain forests of Panama, rapidly growing pioneers suppress the presence of a large number of other species that might enter to colonize small gaps (Hubbell et al. 1999). Larger disturbances, such as those exerted by larger climate change or catastrophic and widespread storms would be of greater interest. Vandermeer, Granzow de la Certa, Boucher, Perfecto, and Ruiz (2000) investigated the role of a large hurricane on diversity and found that the large patches created permitted the invasion of a large number of species. In contrast to the expectations of Levinton's model, such disturbances might forestall extinction. It would be likely, however, that still larger disturbances, such as those caused by major climate changes, would cause wide swaths of extinctions. This would correspond to the large-disturbance tail of the intermediate-disturbance model of diversity.

A notion of steady state can be extended to a consideration of morphological specialization. Specialized species would be expected to occupy smaller areas and have smaller population sizes than generalized species. This would be due to both restricted geographic range and restriction to a narrow spectrum of resources within a community. Their capacity to resist catastrophe is therefore inherently lower than more generalized forms. Specialization would therefore be expected to increase up to the point that the average restriction by specialization to a given population size and area would match the background rate of environmental catastrophes. This would provide a component of the explanation for the commonly postulated inverse association between specialization and species richness.

The two processes of diversity regulation connoted by the models are of course not necessarily independent. Both may contribute to an explanation of overall taxonomic richness. The competitive speciation model cannot be the complete answer as we know of environments, such as soft sediments, whose structural similarity and homogeneity are accompanied by extensive geographic variation in species richness (summary in Levinton 1982a). The bivalve mollusk genus *Macoma,* for example, has 13 species in Pacific coast soft-sediment environments. Although some specialization is apparent, extensive coexistence occurs among intertidal and subtidal species (Dunnill and Ellis 1969). On the east coast of the United States, only two species can be found in the same environment types, with no conspicuous increase of some other ecologically equivalent biotic component. Of course, structural habitat complexity is also a major component in explaining species richness. Within the same overall region, structurally diverse habitats, such as coral reefs and temperate rocky reefs, harbor far more species than nearby monotonous habitats. Niche subdivision resulting from interspecific competition can be seen in structurally complex habitats (e.g., the lizard genus *Anolis* in erect vegetation; Williams 1972); the carnivorous gastropod genus *Conus* in subtidal coral reefs (Kohn 1959), and even in some structurally simple habitats (e.g., mollusks in soft sediments; Fenchel 1975; Levinton 1977; Peterson 1977). Niche subdivision among *Anolis* lizard species on larger Caribbean islands appears to have evolved concomitantly with speciation (Losos, Jackman, Larson, Dequeiroz, and Rodriquez-Schattino 1998). On the other hand, coexistence with no apparent niche subdivision has been documented in structurally complex environments (e.g., intertidal coral reef benches, Levitan and Kohn 1980). The apparent pervasive occurrence of interspecific competition in nature (e.g., Schoener 1983) does not guarantee persistent niche subdivision but may simply involve continuous competition for the same sites, with priority effects determining dominance, as required by the stochastic area–population effect model.

A potential weakness of models of area and diversity is the potential for refuges. The species-area effect might appear to apply to continental shelf benthos, especially during periods of regression. If so, the stochastic species-area effect should apply as well. But what if regressions failed to eliminate all representatives of a taxon? Jablonski and Flessa (1986) pointed out that a large proportion of the living marine shallow water biota can be found on oceanic islands. Even a global eustatic lowering of sea level would fail to eliminate even a small proportion of the world's shallow water marine fauna, because so little is confined to the shelves. For example, just 2 of the 22 islands they examined harbored 78 percent of the world's shallow-water Recent families. An entire eradication of the living shelf fauna would only eliminate ca. 13 percent of the world's families.

Coordinated stasis and ecological locking? Boucot's concept of EEUs implies that a group of species, or at least genera, persist for some period of time owing to a stabilizing force that lasts for millions of years (Boucot 1978; Boucout, Ivany, and Schopf 1996). Brett and Baird (1995) argued that community stability of several million years is commonplace in the fossil record. They claim that periods of coordinated stasis are punctuated by short, rapid shifts when extinction, speciation, and morphological evolution are accelerated, within a period less than 10% of the longer periods of stability (Brett, Ivany, and Schopf 1996). As mentioned above, the stable periods of species occurrence may merely reflect the presence of a few dominant species adapted as members of functional groups to a common overall environment and perhaps interacting to some degree. It would also make sense that species with greater dispersal capabilities would have longer durations and would contribute to a pattern of extended survival; dispersal would dampen local differentiation, thus encouraging stasis.

Coordinated stasis derives from Brett and Baird's (1995; Brett et al. 1996) study of Appalachian Devonian nearshore marine clastic sediment communities. During intervals of 3 million to 7 million years, the degree of turnover of species was much lower than during the relatively short transitions between these intervals. It is not entirely clear whether these changes are restricted to the Appalachian basin represented by these rocks or whether they were more global in extent in coeval basins throughout the world ocean. Episodic changes correlate with basinwide changes that are reflected in lithologic change, which implies some degree of change in the sedimentary regime. Thus, the physical environment appears to be the driving force behind the bimodality observed by Brett and Baird.

Community interdependence, such as the evolution of competitive niche structure and mutualisms, might provide a stabilizing force that buffers the EEUs against change (Ivany and Schopf 1996). The role of species interdependence in the long-term persistence of species assemblages has been argued to be so tight that species are "ecologically locked" and strongly resist the invasion of other species (Morris 1995; Morris, Ivany, and Schopf 1995). The notion of stability driven by a set of coexisting species dominated the thinking of community ecologists for many years, but marine benthic ecologists have become more impressed in recent years with the lack of such competitive equilibria (Underwood and Denley 1984). There is, however, a theoretical basis for arguing that diverse communities might be able to resist major invaders and, therefore, major change. With more species, there are more possibilities for monopolization of resources, which would make it harder for an exotic species to invade (Tilman 1999). With only a single species, a local disastrous population decline opens up space for invasion, but with many species, the decline of one native species might be made up by the increase of others.

If we consider some common modern environments, we can imagine the stability arising principally from a local environment that is undisturbed by major climatic changes, monopolized by a few dominant species adapted to common substrates, and other rarer species. On rocky shores, for example, a remarkable similarity of community structure may persist over thousands of kilometers of shoreline on the west coast of North America (Paine 1969), and some features of rocky shore community structure are worldwide in extent (Stephenson and Stephenson 1972). It is common for dominant species in nearshore marine benthic communities to be strong interactors in food webs (Estes and Palmisano 1974; Paine 1966); to be bioengineers, affecting substrate structure (Levinton 1994); and to be major competitors for substrate dominance (Levinton 1977; Paine 1966; Seed 1969; Woodin 1974). The strong interactive properties of dominant species usually transcend a good deal of environmental change; indeed, the common species are buffered against change by their very abundance and ability to rapidly increase in population size and dominate a community. For example, sea otters were nearly absent from eastern North Pacific kelp forests for many years, which must have caused major changes in community structure (Estes and Palmisano 1974). The increase in otters in recent years probably caused some increase in kelp via indirect food web effects, but other factors such as regional disturbance, strong shifts in echinoderm larval recruitment, and localized disturbance probably were equally important in causing a number of rapid shifts (Dayton and Tegner 1984; Ebeling, Laur, and Rowley 1985; Harrold and Reed 1985). Thus, the extreme extent of environmental disturbance and local extinction does not drive whole communities to extinction. Indeed, the major players are surprisingly resilient to enormous change of environment and abundance of other strongly interacting species. These considerations at least suggest that common species in the marine fossil record might live and coexist for long periods of time. No stabilizing mechanism would be required.

The success of invasion of marine communities is too common to ignore, even if much of it is caused by humans these days. Ecological locking seems dubious, given the common success of recent invading species into freshwater and marine invertebrate communities (Carlton and Geller 1993). The zebra mussel is a fascinating case in point. It invaded a rich North American malacofauna and appears to be superior to native unionid bivalve species in substrate occupation and perhaps feeding rate (Baker, Levinton, Kurdziel, and Shumway 1998; Strayer 1991). The gastropod *Littorina littorea* invaded eastern North America and now is a dominant species on rocky shores (Brenchley and Carlton 1983). I would suggest that one would be hard pressed to discern the current ecological position of *L. littorea* from an "ecologically locked" community, because it fits so well in a vertical zonation scheme. Although it may have reorganized parts of local habitat structure (Brenchley and Carlton 1983), there is no evidence that any local species were driven to extinction. Although the invasion of species can have strong and variable effects (Berman, Harris, Lambert, Buttrick, and Dufresne 1992), it is not clear that successful invasion occurs usually because of ecological superiority to resident species (Berman and Carlton 1991). So many invaders do well that the notion of ecologically locked marine communities is readily falsified, unless the Paleozoic differs from the Recent.

The stability implied by coordinated stasis extends to a claim of morphological stability, which might be related to punctuated equilibrium, especially if the short periods of turnover are times of branching. Punctuated equilibrium would not apply if the turnover periods merely involved sudden morphological shifts within a nonsplitting species lineage, which would be compatible with a standard model of rectilinear selection change.

Morphological constancy is a difficult notion, as we discussed in chapter 6. As shown by Gingerich (1993a, 1993b), a population may exhibit no net morphological trend but still might have very rapid changes in morphology, even compatible to periods of strong selection in laboratory populations. An examination of two abundant brachiopods in the Devonian Hamilton Group showed that although morphology did not trend in any particular direction, there were a number of oscillations over the approximate 6-million-year interval represented by the sediments (Lieberman, Brett, and Eldredge 1995). It is not easy to relate morphological constancy between an individual population to the long-term history of a species. Stabilizing selection must have a prominent role in averting continual monotonic evolutionary change. This would be no surprise, as we would not expect a sudden shift in size to result in mussels the size of a barn. Stabilizing selection or at least common selection regimes may cause widespread similarities in marine species, despite molecular evidence for subdivided population structure (Karl and Avise 1992). Dispersal, even at an extremely low level, will only enhance the possibility of broad-scale similarity in morphology of widespread marine species (Slatkin 1987). Thus, in a generally sedimentary environment it would not be surprising to find temporal morphological constancy over many millions of years, perhaps with some wobble.

If the environment fluctuates unpredictably, one might expect the evolution of phenotypic plasticity to dominate, as opposed to specialized morphotypes that shift from one time period to another. In recent years, a remarkable amount of plasticity has been found as a response to substrate and food (see Meyer 1987; Padilla, Dittman, Franz, and Sladek 1996; Smith and Palmer 1994; West-Eberhard 1989). This is the major interactive force that translates stabilizing selection into long-term stability of phenotypes, as a single genotype can provide a range of phenotypes, with no necessary long-term evolutionary change. Lieberman and Dudgeon (1996) argued that the abundant evidence for disturbance and rapid shifts in marine communities argues against the role of stabilizing selection. Actually, it is rather the opposite. Such shifts will select for phenotypic plasticity, the inevitable bedfellow of stabilizing selection in a variable environment.

In chapter 6, we mentioned a case in which sedimentary cyclicity can be related to morphological trends in Jurassic ammonites (Bayer and McGhee 1984). Repeated transgressive–regressive cycles stimulated repetitive morphological trends, which resulted in anagenetic species strings. It may well be that a number of basinal histories resemble such a case. The ammonite data are unfortunately not complemented by community data; this would be a very useful contrast to the interesting results of Brett and Baird.

The jury is still out on whether coordinated stasis is a general phenomenon, and differences of temporal scale among studies will hamper comparisons (Miller 1997). At present, the few careful studies are conflicting in result. Brett and Baird's results in the Devonian were not repeated in earlier eastern U.S. sedimentary rocks of the Middle and Upper Ordovician (Patzkowsky and Holland 1997). Fossil assemblages did conform generally to a temporal succession of biotas interrupted by distinctly higher overturn, but there also was considerable turnover within the biotas with lower overturn, which does not conform to the expected coordinated stasis pattern. A lack of ecological fidelity and only broad overlap between coexisting species further did not fit with the idea of ecological locking. Stanton and Dodd (1997) similarly found little evidence to support coordinated stasis in Pliocene shelf faunas of the western United States. Faunas changed gradually rather than in sudden jumps, intervened by relatively long periods of stability. Similarly negative results have been obtained for Cenozoic mammal assemblages (Alroy 1996). Origination and extinction rates of mammal species were not correlated, once an apparent artifact of species appearing and disappearing within the same minimal stratigraphic interval was subtracted. The majority of extinction conformed to a single, invariant, underlying rate, but origination rates show many well-defined pulses. Pulses of origination within particular orders of mammals did not coincide fully. Alroy argued that the largest peaks of origination may have been mediated by the rise of key adaptations within particular groups and not by the general opportunity to fill niches opened up by extinction. His results argue against the idea of coordinated stasis.

Biogeography, Provinciality, Diversity, and Diversification

Dispersal, speciation, and morphological evolution. Dispersal counters the effect of local selection and drift, which, in turn, reduces the probability of local differentiation and speciation. Thus, chromosomally or genically polytypic species usually have restricted dispersal ability (chapter 3), although strong local selection can generate regional differentiation, as in estuaries (Levinton 1980). As might be expected, biogeographic range is also related inversely to species richness. Jackson (1974) found that species indigenous to very shallow water had far larger biogeographic ranges than did deeper-water species (excluding the deep sea); the former habitat is much lower in species richness. Dispersal potential seems to be greater in nearshore habitats, an expectable adaptation to higher local population extinction rates (Jablonski and Valentine 1981). The evolution of provinciality may partially result from reduced dispersal, but the increase of within-province habitat heterogeneity may also be a factor. Species richness might be explained by an inverse relationship between regional diversity and geographic ranges of species. In effect, more species could be packed in a given area or lineal stretch of coastline, if their geographic ranges were smaller (Stevens 1989). Smaller freshwater crustaceans (France 1992) and North American mammals (Brown 1995) fit this pattern rather well, but eastern Pacific mollusks do not fit this expectation (Roy, Jablonski, and Valentine 1994).

In the living marine invertebrates, dispersal ability can be related to speciation to a degree. Scheltema (1971) discovered the presence of long-ranging (teleplanic) larvae in the surface waters of the middle and north Atlantic Ocean. Those species with commonly teleplanic larvae were found in both South America and Africa. Sanders and Hessler (1969) found a positive correlation in the deep-sea invertebrates between dispersal ability and species geographic range. A relationship between dispersal ability and regional genetic differentiation can also be seen (Snyder and Gooch 1973), but the magnitude of the latitudinal temperature gradient may play at least as great a role in differentiation (Levinton and Monahan 1983; Levinton and Suchanek 1978). Vermeij (1982), however, showed that predation on a gastropod with limited dispersal induced significant morphological changes but failed to do so in another species with greater dispersal, presumably from habitats lacking the predator. Dispersal from adjacent habitats may increase colonization, but it also reduces the chance for local adaptation.

Unfortunately, our understanding of geographic range changes in the marine environment is generally limited to invasions that are probably facilitated by marine commercial transport. Some species with planktonic larvae have moved quite rapidly along coastlines. The common periwinkle, *Littorina littorea,* probably extended its range from Nova Scotia to the mid-Atlantic within a hundred years (Brenchley and Carlton 1983). The spread occurred at a rate of about 15 to 20 kilometers per year, which is consistent with southward larval dispersal via stepping-stones. The approximate spreading rate of 10 to 20 coastal kilometers per year suggests a limitation of spread by planktonic larval dispersal. Following latitudinal climatic shift in which a warm-water Norwegian fauna moved 1,500 kilometers northward and back, the rate of southward movement of warm-water species was also limited by the rate of dispersal and not by the rate of climatic change (Spjeldnaes 1964).

A consistent relationship among dispersal ability, speciation, and geological duration has been found in fossil studies, principally of mollusks. The marine snail genus *Turritella* in Neogene Atlantic coastal plain sediments consists of two lineages of differing dispersal ability, speciation rate, and morphological differentiation. Dispersal ability can be judged by the size and ornament of the protoconch. The *variabilis* lineage shows evidence of strong dispersal, little cladogenesis, long species stratigraphic durations, and broader phenotypic variability within species. In contrast, the *alticostata* lineage shows evidence of reduced dispersal, extensive cladogenesis, short stratigraphic durations for species, and narrower phenotypic variability within a species (Spiller 1977). Hansen (1980, 1982) found a similar relationship among volutid gastropods. Presumed planktonic forms had greater longevities and could survive several stages of transgression and regression. In contrast, nonplanktonic forms had shorter durations. Fasciolarids and mitrids had planktonic larvae, though they had short stratigraphic durations; this may indicate their relative ecological restriction. Apparently, the relationship can be seen only within groups of ecologically similar taxa. Kauffman (1978), for example, found that oysters had shorter species durations than nuculid bivalves, even though the latter usually have restricted dispersal via a lecithotrophic larva (e.g., Scheltema 1971). Ecological difference may therefore swamp out the mode of dispersal in affecting longevity and speciation.

The limited evidence available from the fossil record is concordant with both theoretical expectations and work with living species. Species with short dispersal distances are more prone to become polytypic, perhaps leading to allopatric speciation. A clade with species having reduced dispersal is therefore liable to have a greater speciation rate. This creates more opportunities for divergent evolution. The reduced survivorship of species with reduced dispersal is not as easy to explain. If dispersal is reduced, gene flow from other populations will not swamp out local divergent evolution. Thus, phyletic evolution is to be expected to a greater degree; some of the short taxonomic durations may reflect the successional species–morphological change bias discussed in chapter 6. It is also possible that species produced under these circumstances are more specialized and are therefore more prone to extinction after an environmental perturbation. Finally, the reduced area occupied would enhance the probability that a given regional change would extinguish the species, relative to broader-ranging species.

Because the available paleontological data follow so well a model of speciation involving polytypic divergence, followed by the evolution of incompatibility in isolation, it is incorrect to state that speciation is the cause of morphological evolution (Stanley 1979). Speciation is the result of divergent evolution, probably stemming from regionally variable natural selection but enhanced by reduced dispersal. This raises the question of whether dispersal itself is under the control of natural selective forces that would help determine the degree of isolation. In the case of teleplanic (long-dispersing) larvae, successful dispersal is simply an accident, because only a trivial proportion of the larvae produced in the coastal populations is liable to find its way across the open ocean. But in most cases, dispersal may be regulated to maximize success. Thus, adaptive changes within populations may be easily conflated with long-term changes that might be thought to be caused by high speciation rates. The temporal increase in Tertiary snails with reduced dispersal is a case in point. As Hansen (1982, p. 372) noted: “The high percentages of low-dispersal forms among the warm-water neogastropods in apparent contrast to bivalves and most other prosobranchs is suggestive of some type of adaptive process.” Thus, individual adaptation could lead to reduced dispersal, which, in turn, leads to speciation. An abundance of species with low dispersal would therefore be the result of individual adaptation and not a process reducible only to speciation.

If the local population is stable and adult mortality is low, life history theory (Stearns 1976) would predict the evolution of reduced reproductive output and selection for increased investment in survival of the adult. Investment in the adult would involve ecological specializations whose rate of acquisition would be enhanced by a decrease in reproductive investment. In turn, reduced production of young would be followed by reduced dispersal, assuming the adults are fairly sessile. As the distribution of dispersing larvae attests, the nearshore environment is more dangerous than offshore sites; dispersal potential in nearshore species is far greater (Jablonski and Valentine 1981; Jackson 1974). In contrast, opportunities for the evolution of reduced dispersal often close the door to successful long-range colonization of new habitats. Species evolving both reduced reproductive investment and increased adult specialization are those whose colonists will probably not be able to find suitable habitats elsewhere or will be unable to successfully move along potential dispersal routes. Mountain passes, for example, present more formidable obstacles to (thermally) narrowly adapted tropical species, relative to the effect of passes on higher latitude forms (Janzen 1967). The Amazon River is a major biogeographic barrier, whereas a river of similar breadth in midlatitudes such as the Mississippi River or Hudson River is no real barrier to dispersal of similar groups. Ecological specialization of the adult and production/dispersal of young are therefore interactive and must coevolve. As a result, speciation is so intimately related to local adaptation that it often becomes fruitless to argue whether speciation is the cause or effect of morphological change.

Do clades with higher speciation rates, or a positive speciation–extinction balance, survive by virtue of their very speciation rate? This is an argument of the *effect hypothesis,* proposed by Vrba (1983). For mollusks, the hypothesis doesn’t fit the pattern presented above. Clades with widespread species tend to speciate at a low rate, and the geological durations of the component species are usually large. It has been generally found that fossil species with broad geographic range are quite long ranging and are far less prone to extinction than are taxa with narrow geographic range (Bretsky 1973; Boucot 1975). Alternatively, clades with species of geographically narrow range tend to speciate at a high rate, and species have shorter geologic durations. An inverse relationship between species longevity and speciation rate may thus result in no net difference in overall longevity between clades that speciate at very different tempos. In many cases, such speciation in fast-speciating clades results in a set of species that are morphologically similar, with no major innovations. This often occurs concomitantly with an increase of provinciality in the marine environment, such as the steady increase in provinciality during the diversification of the Silurian fauna into a highly provincial Early Devonian fauna. Such divergence has been termed *diacladogenesis* (Boucot 1978, p. 569). Increased survival of a high-speciating clade might occur if species are produced with innovations that propel it into a new adaptive zone (*metacladogenesis* of Boucot 1978), which greatly improves the chances of success. But taken alone, this would not satisfy the effect hypothesis, as an additional component of success from adaptation must be invoked. The increased survival of larger inclusive taxa, such as families, could be the result of increased numbers of species per family as diacladogenesis occurs (Flessa and Jablonski 1985). The data provided by Stanley (1979) on the bivalve mollusks suggest that speciation rate alone does not confer success. All of the bivalve families he considered define a linear relationship between the logarithm of time of origin and present-day species richness. It follows from this that newer bivalve families do not have increased speciation–extinction differentials relative to older ones. In other words, there has been no net increase over time of clades with higher speciation–extinction differentials. Hoffman and Ghiold's (1985) analysis of family-level data shows an irregular decline of family origination rate since the Mesozoic.

Many biostratigraphers have investigated the question of speciation and biogeographic range in the context of fluctuations in sea level. Kauffman's (1973) extensive study of Cretaceous bivalve genera suggests that speciation and endemism were both maximized during periods of transgression. He related this pattern to the spreading of colonizing populations over many environments and separated areas as sea level rose. This result is generally concordant with Jablonski's (1979, 1980) study of Late Cretaceous Gulf Coast plain sediments, where maximum endemism was found during transgressive (sea-level rise) phases. On a larger scale, the entire Cambrian period of diversity expansion was a period of overall and continuous transgression (e.g., Boucot 1975). In contrast to these results, endemism is greater in Jurassic bivalves when inundation is at its lowest (Hallam 1977a). During regressive (sea-level fall) phases, maximum separation of marine basins might encourage divergent evolution and speciation. Jablonski (1980) argued that Hallam's result should not be surprising, given the Jurassic situation of relative continental assembly. Under such circumstances, there would be few opportunities for isolation without regression. In the Cretaceous, the continents might have been sufficiently separated that inundations brought colonists onto a series of isolated continental shelves. Regressive sequences are better preserved in the fossil record than transgressive ones. This would be particularly true of short-term events. As species with broader dispersal potential are to be found near shore, regressive sequences may have broader ranging species simply because of the relative frequency of preserved nearshore habitats. There is thus a possible bias against sampling endemic offshore species during regressions.

A role for population size? The probability of extinction should increase as population size decreases. Thus, broad geographic range could reduce extinction either by virtue of large population size or owing to an extensive geographic range that is resistant to widespread habitat extinction. Population size per se, however, may depress extinction, independent of geographic range. Stochastic fluctuations in population size would more frequently cause extinction in species with small populations. Deterministic factors such as disease, changes in the productivity regime, predation, and disturbance would also fall more heavily on species with small population size. This was a major theme in Boucot's (1978) monograph on evolutionary stability. His analysis of fossil abundance suggested that common species were unusually longevous. There is often a correlation between abundance and geographic range; this makes it difficult to distinguish between the two factors in explaining extinction. Among Pacific Pleistocene bivalve mollusks, small siphonate bivalves are more endemic than large bivalves, yet have significantly better survival (Stanley 1986a). This may be related to the presumed large population sizes of species with small body size, although Stanley presented no direct evidence to support the correlation in the groups he studied. In contrast, Pectinidae, whose geographic ranges are usually large, have high rates of extinction. Stanley attributed this to their vulnerability to predation. He also reinterpreted the lower extinction rate of deposit-feeding nuculid bivalves (Levinton 1974) as the result of large population size, as opposed to trophic group. It is premature to single out predation on scallops as the only factor. In recent years, it has become apparent to marine ecologists that disease and changes in phytoplankton dominance (e.g., red tides and brown tides) are major sources of population decline.

Area, provinces, and diversity. During the Phanerozoic, sea-level coverage and exposure of terrestrial environments varied extensively. Paleontologists have recognized these patterns by facies maps indicating distributions of environments. Thus, the marine regression in the Middle–Upper Devonian in New York State is recorded well by a sequence of sediments from fully marine to terrestrial–freshwater in origin. Changing geographic relationships of the fauna and flora have also been traditionally used to understand paleobiogeographic relationships.

The confirmation of the processes of sea-floor spreading and continental drift provide immediate explanations for many biogeographic problems. The pervasive cosmopolitanism of Early and Middle Mesozoic faunas can be related to a period of continental assembly. The gradual increase in provinciality from the Jurassic to the Cretaceous (Kauffman 1973; Stevens 1973) could be related to the breakup of the supercontinent Pangaea and the establishment of north–south trending continental shelves spanning large ranges of latitude (Valentine 1971a). The large present-day latitudinal variation in climate is unusual in Phanerozoic history and may date back to the major cooling event toward the end of the Eocene (Shackleton and Kennett 1975; Valentine, Foin, and Peart 1978; Wolfe and Hopkins 1967). Presumably, as the evidence accumulates, paleogeographic maps (e.g., Scotese, Bambach, Barton, Van der Voo, and Ziegler 1979; Smith and Briden 1977) will permit an association between continental dispersion and biogeographic subdivision. The current evidence suggests that the spatial arrangement of the continents has been continually changing, and movements have significantly affected the climatic history of individual continental blocks (discussion in Bambach, Scotese, and Ziegler 1980).

Some of the Phanerozoic changes in taxon richness can be related to a large degree to changes in the degree of *provinciality.* If we take the species area effect (MacArthur and Wilson 1967) as given and constant, it is easy to calculate that as one large province is divided in two, reductions of area are more than compensated for by the increased total species richness as long as dispersal between areas is limited. The Silurian Period, for example, was one of extreme cosmopolitanism, with one province of approximately 90 articulate brachiopod genera in the North Silurian Realm. In the Ludlow (Upper Silurian), two provinces can be delineated, with about 90 genera in each province. In the Devonian, the number of provinces increased to six; the total numbers of articulate brachiopod genera increased to about 350 on average (Boucot 1978, p. 577). During the Frasnian (Late Devonian), this provinciality decreased relatively suddenly, and generic richness returned to 93.

The onset of the Permian extinction was also marked by a decrease in numbers of provinces, and the Early Triassic marks a nadir of provinciality in the Phanerozoic (Valentine et al. 1978). During the end of the Paleozoic, geographically restricted bivalve genera succumbed before more widespread genera, suggesting that the overall environmental change was filtering out those forms that define provinciality in the first place. Newell (1952) argued that the extinction was related to the major fall in sea level. Shallow marine seas were reduced from a coverage of 40% of their possible extent in the Early Permian to less than 15% in the latest Permian and then expanded to 34% in the Early Triassic (Schopf 1974). Reduced rates of sea-floor spreading may have been responsible for a lowering of ridge activity, depression of deep-sea bottoms, and the consequential large-scale marine regression (Valentine and Moores 1971). The significant reduction in area, coupled with continental assembly of Pangaea at the end of the Permian, might have increased extinction rates and would have homogenized the fauna owing to the possible presence of more intershelf dispersal possibilities. In contrast, the Pleistocene reduction of area covered by the sea was far lower, and on the basis of area alone, the modest marine extinctions are therefore not surprising from this point of view (Wise and Schopf 1981). Area reduction itself might not be a potent agent of extinction (Jablonski 1985, Jablonski and Flessa 1986). Sea-level drops would hardly affect the shallow-water habitat distribution of oceanic islands, where most modern families are widely distributed. Sea-level drop may just be a correlate of another change.

The changing spatial relationships generated by continental drift and sea-level fluctuations must have had important influences on climate. Valentine's (1971a) theory of climate change generated by continental assembly and fragmentation attempted to relate climate and sea level to sea-floor spreading. Periods of continental assembly were envisioned as times when interior continental climates were severe, affecting the continental shelf faunas. In contrast, times of fragmentation were times when the continents' climate was more moderate owing to ameliorating marine conditions; this permitted the buildup of shallow-water diversity. Although the post-Permian expansion may fit this pattern, evidence from the Paleozoic does not seem to show an increase in continental fragmentation during the Early to Middle Paleozoic. Indeed, the continents were maximally fragmented and arrayed along the equator during the Cambrian (Scotese et al. 1979). Continental drift and arrangement nevertheless has had profound effects on climate and probably extinction. During the Ordovician and Silurian Periods, Gondwanaland drifted southward from its Cambrian position at the equator and came to rest on the geographic south pole. This coincides with the Late Ordovician glacial tillites that have been found in North Africa and with a large reduction in the degree of marine provinciality relative to the Early Ordovician. In the Cenozoic, the spatial arrangements of the continents about the Pacific and Atlantic Oceans made for a quite different climatic history (Briggs 1970). The North Atlantic was a more enclosed basin and was far more severely affected by the Late Cenozoic polar cooling. The Pleistocene initiated severe enough climates to cause a major molluscan extinction in the southeastern United States shelf, whereas Pacific American faunas showed no increased extinction (Stanley 1986b; Stanley and Campbell 1981).

What is the tempo of change as provinces are homogenized? If modern mammalian faunas are any indication, it seems to be the case that readjustments and changes of diversity in isolated areas are rapid relative to the pace of change in climate and continental rearrangement. Flessa (1981) found that as much as 70% of the degree of similarity in mammalian genera among continents can be explained by present-day distance, longitudinal separation, and area, in order of decreasing importance. Historical effects do not obscure the present-day pattern.

The effects of increasing access between biogeographic realms can be illustrated by the large-scale interchange of mammals between North and South America after the Pliocene establishment of the Isthmus of Panamá, following the disappearance of the Bolivar Trough marine barrier (Marshall, Webb, Sepkoski, and Raup 1982). Before the interchange, there was long-term stability in numbers of mammalian families. As a probable result of North America's initial higher taxon richness, more taxa moved from north to south than in the reverse direction. In South America, where taxon richness now exceeded previous "steady state" levels by more than 50%, there was about a 70% increase in extinction rates. Descendants of the North American invaders participated in an evolutionary radiation, resulting ultimately in an overall richness higher than previous levels. Mammalian diversity is now higher in South America, in contrast to the situation previous to the exchange. This suggests that area does have an effect on regulating diversity but that evolutionary changes can impose a significant overprint on diversity.

Geographic locus of evolution and innovations. The origin and evolution of biotas have often been placed in a geographic context. Interpretations have usually been based on the presence of gradients in taxon richness, especially latitudinal increases toward the tropics (Pianka 1966). These have been used to infer centers of origin in loci of higher diversity, from which colonists have moved toward less hospitable habitats. This general argument may have some validity, but it has been called into question by evidence adduced from the fossil record. A major element of early Cenozoic southern hemisphere marine faunas appeared first in high latitudes and then spread to low latitudes as the climate became cooler (Zinsmeister and Feldmann 1984). The same story has been claimed to apply in the origin and spread of early Tertiary floras (Hickey, West, Dawson, and Cho: 1983), but the stratigraphic correlations have been questioned (Spicer et al. 1987). A similar pattern of origins in what

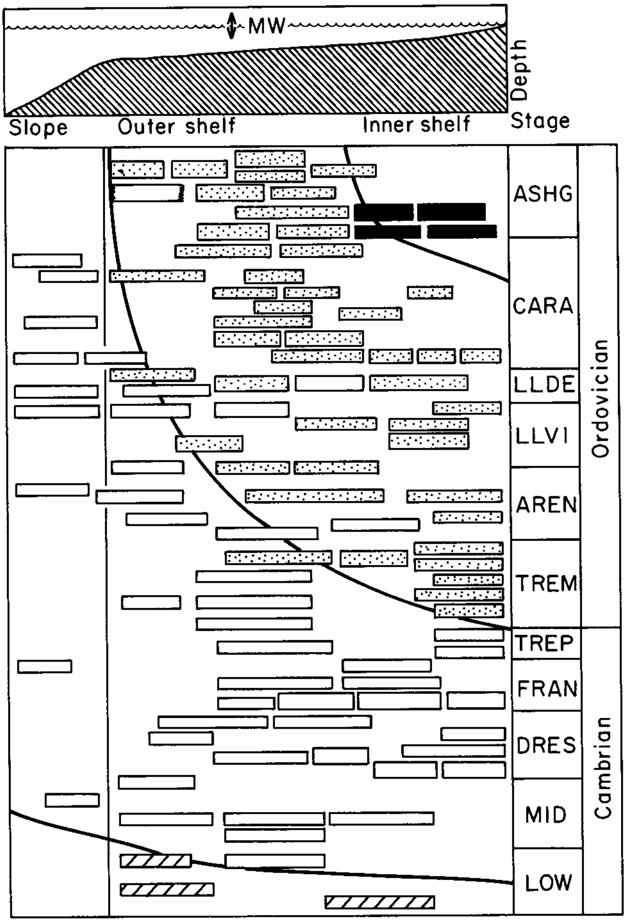

Figure 7.11. Depth distribution of successive Cambro-Ordovician fossil communities. Lines describe a qualitative fit of the time-transgressive nature of offshore spread of the communities. (After Jablonski et al. 1983.)

seem to be extreme environments has been found (Jablonski, Sepkoski, Bottjer, and Sheehan 1983; Jablonski and Bottjer 1990; Sepkoski and Sheehan 1983) in the evolution and appearance of marine benthic faunas. In Cambro-Ordovician benthic communities, new assemblages appear first in shallow-water facies and then spread to offshore depths (Figure 7.11). The rate of appearance of post-Paleozoic ordinal-level marine taxa is similarly higher in onshore habitats (Jablonski 1993), again suggesting an association of innovation with environmental uncertainty.

These results are paradoxical in the light of our explanation above of provinciality, which would predict that morphological specializations and innovation would come from more stable habitats (e.g., offshore in the marine environment). The Cenozoic high-latitude heterochroneity of faunas and floras is more understandable in light of the fact that the overall Cenozoic world climate became progressively cooler, especially after the Late Eocene, making spread from high latitudes expectable. But the spread from inshore habitats toward offshore is more difficult to explain because offshore habitats harbor more species and clades with higher speciation rates. It is possible that we should not be looking at species-level diversity or stability to explain the onshore fount of innovation. It may just be that there are more habitat types in the inner shelf, which promotes selection for new innovations.

We might not expect more offshore faunas to invade inshore, as they probably lack the degree of ecological flexibility required to make it in the inner shelf. The possible predominance of the reverse invasion route is not so easy to explain. In Lake Baikal, an ancient lake with extraordinary deep-water benthic endemic diversity, the deep-water forms are also believed to have arisen from shallower water, near the break in slope (Kozhov 1963). It may be that the habitat extinction rate in shallow water is sufficient to continually permit new evolutionary experiments to occur, some of which are successful enough to colonize outward. The more diverse stable habitats may have biotas too persistent to permit the survival of species much different than their ancestors. An unstable habitat may normally select against the gradual development of a specialized biota but would not prevent the origin of new innovations.

The specialized nature of the offshore fauna may also make them more closed to innovations and more prone to mass extinction. Alternatively, the offshore biota may be dominated by groups with higher characteristic extinction rates (Sepkoski 1987). Bretsky (1969) showed an increased offshore community extinction rate through the Paleozoic. This same effect has been documented in more detail through the 5-million-year Frasnian (Upper Devonian). Although replacements occur in both near and offshore communities, the effect was more dramatic offshore (McGhee 1981). Extinctions of the offshore fauna may provide opportunities for invasion from inshore habitats.

Mount and Signor (1985) argued that one must distinguish between the successful spread of ancient biotic assemblages and the actual first appearances of innovations. Their study of the Early Cambrian shelly and trace fossils of the White-Inyo Mountains shows that first appearances occur in offshore habitats. A further examination of first appearances of Paleozoic higher shelly taxa with distinctive morphologies shows a similar lack of fidelity to nearest shore habitats (Signor and Mount 1986). This may suggest that those innovations that appear nearshore are more successful, but it may also call into question the linkage between long-term movements of whole biotas (as documented by Sheehan and others) and the first appearance of innovations in given groups.

As usual, we seek hypotheses that can relate properties of the physical environment to evolutionary events. Jacobs and Lindberg (1998) established just such a relationship with apparent success. Paleozoic and pre-Turonian Mesozoic oceans are notable for the common occurrence of anoxic or dysaerobic deeper and outer shelf waters. After the Turonian, there is evidence for more aggressive deep circulation, which perhaps increases oxygenation. In today's oceans, vertical replenishment of oxygen to the deep is strongly influenced by the strong latitudinal temperature gradient, and deep ocean water is derived from high-latitude surface sources that sink and move toward the equator at depth (Levinton 1995). Because glaciation is not a continuous factor in post-Turonian environments, it is not clear why deep oxygenation is so much more common. But this divide appears to mark the time at which inshore innovations (= ordinal appearances) cease to dominate nearshore.

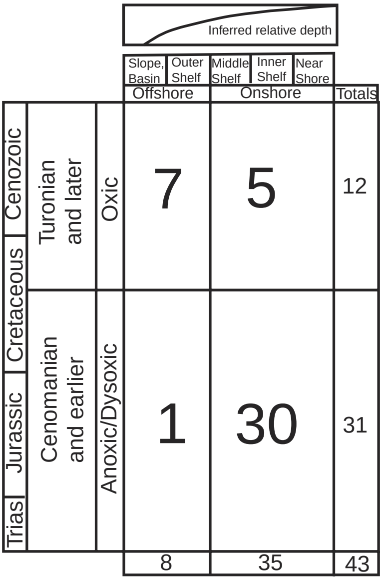

Figure 7.12. The time and environment of first occurrences of orders of marine macroinvertebrates. The larger numbers form a contingency table whose contents are nonrandom. (After Jacobs and Lindberg 1998.)

Before the Turonian, most of the ordinal appearances occur inshore; afterward, they are more evenly divided between onshore and offshore (Figure 7.12), which would suggest that anoxia simply limited offshore life before the Turonian. Stress is not compatible with innovation and proliferation of species. This result is very exciting, as it is a rare case where paleooceanography can be linked to evolution.

Diversity gradients in modern biotas may be deceiving, as they can be the result of extinctions in peripheral environments rather than a reflection of a depauperate peripheral biota, periodically colonized by a rich tropical biota. The center of diversity in Pacific coral reefs, for example, may be the result of deterioration of climate through the Cenozoic that may have mainly affected the periphery of the province (Newell 1971). Studies of coral reefs (Stehli and Wells 1971) and Foraminifera (Stehli, Douglas, and Kafescegliou 1972) demonstrate that mean longevity of genera increases toward high latitudes. The oldest genera of Pacific corals, for example, are found throughout the province, whereas younger genera may be found toward the center. This may involve selective extinction of younger forms at the periphery of the province, but it may also signify that older, more widely adapted genera are more likely sources for repeated origins of descendants. This is the likely basis for Kaufmann's (1933) concept of a *conservative stock* that survives for a greater period and gives rise to clades of probably higher diversification rates. Groups with low speciation rates are ultimately the survivors in evolution and the repeated progenitors of new radiations. The unspecialized globular Foraminifera dominating high latitudes are the progenitors of repeated radiations of more specialized forms that may accompany vertical structuring of the water column (Lipps 1970). Unspecialized forms survive well in peripheral environments and would survive the inevitable extinction that would be brought on by a radical homogenization of water column structure.

If cladogenesis is greater in the tropics, giving rise to higher diversity, we might expect that there would be greater opportunities for evolutionary innovations. With larger numbers of species, the potential for species interactions and the evolution of new mutualisms, predator and prey specializations, and so on, would be expected to be more frequent (Futuyma 1973), although the expected frequency of such novel features is not so clear (Jumars 1974). Are the tropics a tangled bank, spawning evolutionary innovation? The marine fossil record supports this. In an analysis of ordinal-level taxa, Jablonski (1993) found new appearances to be far more frequent in the tropics, which suggests that the tropics are not a museum but a factory of evolutionary novelty.

Extinction and Mass Extinction

Mass extinction and background extinction. We have discussed the nonrandom pattern of diversification of the marine and terrestrial fauna and flora. Strong temporal changes in taxon turnover were observed first by Newell (1952, 1967), who found peaks of activity in the Ordovician, Carboniferous, and Jurassic. Declines in standing taxon richness were simultaneous and relatively rapid among distantly related taxa, although increases were not so obviously coordinated. If we return to Figure 7.4, we can see five conspicuous and precipitous drops in diversity, the most dramatic occurring at the end of the Permian. Raup and Sepkoski (1982) analyzed overall extinction rate at the family level and found that four events fell outside a one-sided 99% confidence interval from the mean extinction rate trend: Ashgillean (Upper Ordovician); Frasnian (Late Devonian); Guadalupe–Dzhulfian (Late Permian); and Maastrichtian (Late Cretaceous). The Norian (Upper Triassic) fails this test, but its widespread occurrence forces us to include it in the “big five” (see Table 8.1). Benton (1995) analyzed the database reported in *The Fossil Record 2* (Benton 1993), a compilation of stratigraphic ranges of a wide variety of taxa produced by a wide variety of specialists. Inspection of extinction rates revealed peaks in the same times identified by Sepkoski and, indeed, by paleontologists traditionally.

The big drops, *mass extinctions,* are to be distinguished from *background extinction,* which refers to the remainder and overwhelming majority of extinctions. Although the big five are conspicuous, other smaller mass extinctions have been recognized. About half of the marine genera disappeared in the Lower Cambrian, and archaeocyathid reefs were decimated, perhaps owing to widespread marine anoxia (Zhuravlev and Wood 1996). Another possible anoxic event caused a major extinction at the Cenomanian–Turonian boundary (Upper Cretaceous) (Harries and Kauffman 1990), although lowered productivity (Paul and Mitchell 1994) and global cooling (Hallam and Wignall 1997, p. 183) might have contributed. Depending on whom you read, you can subtract or add a few to this list of (now) seven.

Statistical tests of mass extinction do not inspire confidence, because they combine many taxonomic groups of complicated taxonomic structure, reify them to independent data points, and usually analyze them using the assumptions of parametric statistics. Because the groups are enmeshed in a phylogenetic tree structure, it is not easy to reckon the degrees of freedom in such analyses (Harvey and Pagel 1991; Patterson and Smith 1989), and distributions of extinction events are usually skewed toward many events of extinction rates of a few percent and are not Gaussian in shape, although corrections are available for this (Raup 1991b). Raup and Sepkoski's (1982) test is therefore suggestive, but it depends on parametric statistics, which require distributional standards that the data do not meet. Hubbard and Gilinsky (1992) used bootstrapping to reanalyze Sepkoski's data and found evidence to confirm the end-Ordovician, Permian, and Cretaceous extinctions, but they could not confirm the other two. Their parametric analysis identified 12 events, including the big five and others that have been thought to be major extinctions. Although the nonparametric bootstrapping approach is better suited to nonnormal distributions, one could question its statistical power. Failure to find a statistical difference surely cannot be used as evidence to affirm that a phenomenon does not exist at all, only that it cannot be identified.

To properly estimate any extinction event, we would like to know minimally: (1) the number of taxa that become extinct, (2) the total pool of taxa from which a fraction disappear, and (3) the time span over which the extinction occurs. Various types of extinction coefficients could be calculated from these three parameters (Jablonski 1994, 1995).

It may seem inappropriate to fix on mass extinctions, which are atypical end members, but I guess we generally think along these lines: If we can't characterize these events, will we be able to explain the smaller extinctions that were far more common in the history of life? I am not sure I agree with this justification, because it sets apart the pattern and mechanisms behind mass extinctions as qualitatively different from all the others, with no continuity to smaller extinction events. If mass extinctions were caused by qualitatively different events such as heightened episodes of global climate change stimulated by extraterrestrial impacts or very unusual increases in volcanism, then maybe we can justify such a distinction. But if mass extinctions are more or less larger-scale or even global versions of what might happen on a more local scale (extinctions stemming from, e.g., local tectonism, anoxia, regional sea-level change), then maybe we can extrapolate what we learn about them to smaller scales, and vice versa. There is some reason, however, to believe that the big five were distinctive and that the effects of extinctions during these times transcended those of more mundane times (Jablonski 1986, 1994). But this difference may be more apparent than real (Miller 1998). If we focused on times of heightened turnover in taxon richness that are confined to basins (e.g., Brett and Baird 1995), we might see mass extinctions writ small.

If an extinction event is a statistical outlier, then how could we justify a separate category, requiring perhaps a set of extinction mechanisms that differ qualitatively from background extinction. This question opens up a can of worms. There has been a good deal of debate about what a statistical outlier really is and whether mass extinctions are really different from lesser periods of extinction (Hoffman 1989a,b; Quinn 1983). If we assembled extinction rates into a frequency distribution curve, we might argue that the mass extinctions sit squarely on the tails of some expected probability distribution, or a kill curve. The distribution of risk of marine genera consists of groups with mainly low risk, along with some of much higher risk (Raup 1991b). With no mechanistic model in mind, it is not clear whether the somewhat bumpy distribution of extinction rates of marine genera is smooth or discontinuous, and we have no idea of the distribution for species. If we have to wait 100 million years for a mass extinction, are we waiting for an intense version of the same stuff or a truly distinctive event? This question would have meaning only if one cause, with varying intensity, were behind all extinctions.

As much as such a distribution of extinction rates could be imagined, in the context of the time that they occur, mass extinctions are clear and major drops in taxon richness, distinct from extinction rates in the time periods before and after. The Permian appears as a sharp trough in an otherwise clear pattern of expansion since the early Paleozoic. The same can be said for the end-Cretaceous extinction. But numbers really tell only part of the story. A criterion based on outliers alone would stretch the confidence we have in our statistical assessments too far and should be only a means of screening for candidates. To qualify, mass extinction events must have the following features:

1. The number of taxa becoming extinct is significantly greater than in times of other extinctions.
2. The decline is concentrated in a small fraction of the Phanerozoic (e.g., less than a series).[2] Some would object if the decline occurred in more than one episode, even if they were concentrated in time (e.g., Hoffman 1989a, 1989b). Oddly, this would exclude the Permian mass extinction, which occurred over a period of at least 5 million years (Erwin 1993), although the bulk of the species disappeared in less than 1 million years (Bowring et al. 1998; Jin et al. 2000).
3. The extinction is broad-based taxonomically, affecting many distantly related taxa that have not arisen in the same time period as the decline.
4. The extinction affects many different biomes, perhaps not equally. For example, a mass extinction would not be confined to epibenthos on hard surfaces of a region, as opposed to coeval soft-bottom benthos living in the same area.
5. The extinction is geographically widespread – most likely global – in extent.
6. Mass extinction may be caused by mechanisms qualitatively different from background extinctions, but it may be caused merely by “much more of the same” (e.g., anoxia, climate change, unusually large extraterrestrial impacts).
7. Mass extinction affects taxa differently than during other extinctions; small-scale influences on the degree of extinction, such as geographic range, are swamped during mass extinctions (Jablonski 1986).
8. The recovery period following the mass extinction marks either the rise of new taxonomic groups, the expansion of formerly rare groups, or complete reorganizations of ecosystem structure.

Figure 7.4 masks two important issues in quantifying the degree of extinction. First, the extinction event is characterized as a loss. But the nature of loss is unclear, as it may result from declining speciation rates, increasing extinction rates, or both (see next section). Second, taxonomic structure influences our perception of loss. Species-level taxonomy is not sufficiently well developed to be useful in such analyses (Jablonski 1995), and family-level taxon richness has been used as a surrogate. A more recent generic-level analysis has yielded results that are similar to those at the family level, which sug-

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[2] The rocks corresponding to a geological period constitute a *system*. Successive subdivisions of a system are *series* and *stages*.

gests that the species, generic, and family-level taxonomic levels are all correlated and that the latter two probably estimate species-level richness (Sepkoski 1993).

To estimate species-level loss from family loss, Raup (1979) used a rarefaction technique based on the sampling curve that relates the number of species collected at random to the number of families recovered. These are the startling results: Over 95% of the marine (readily fossilizable) species became extinct at the end of the Permian, and the others of the big five took similarly big hits, 75% and more. The Permian was also bad for families (ca. 50% loss), but the others hovered around 20% (Jablonski 1994).

Extinction rates are biased in several respects. First, the rarefaction approach assumes the we can homogeneously extrapolate from families to species. But, for example, certain families may be much more prone to extinction, owing to their presence in a particularly vulnerable habitat (e.g., coral reefs during a cooling event). In such a case, rarefaction will tend to underestimate the species level extinction (Raup 1991b). Second, it is often difficult to estimate the time span over which extinction occurred, owing to strong uncertainty in the time span of geological stages, which is often the crucial level at which extinction is assessed. This is particularly a problem in the early and middle part of the Paleozoic, where time estimates of stage lengths are difficult to estimate with certainty (McGhee 1996). Within stages, rates are especially difficult because of uneven rates of sedimentation, which make it invalid to assume a linear relationship between meters of geological section and time. For example, during a final flood stage of a transgression of the sea, sedimentation rates are often very low, and much time may be compressed in a very small geological section (Hallam and Wignall 1997). Finally, to get a percent extinction estimate, we must have an accurate estimate of the total pool, which becomes more and more difficult as environmental heterogeneity increases sampling difficulties and as preservation is incomplete in different geographic areas.

The estimate of extinction is plagued by other factors as well. Worst of all, the incompleteness of the fossil record imposes biases that cloud an assessment of the tempo and degree of a mass extinction. During the Permian, an enormous regression of the sea resulted in the deposition of few marine deposits and correspondingly few marine fossils. As a result, a number of taxa appeared to become extinct, but they reappear in the Triassic, much as Lazarus was raised from the dead. *Lazarus taxa* may be explained by poor preservation in all facies, resulting in poor sampling of species, even those that really existed during the low point at the end of the extinction (Jablonski 1986). Even if appropriate sedimentary rocks are widespread, reductions in population size may make any species more resistant to successful sampling (Hallam and Wignall 1997, p. 15). Alternatively, there may be localized havens in which such taxa may survive, but these refuge environments might escape preservation (Kauffman and Erwin 1995). In any case, extinction is overestimated. The problem is compounded by so-called *Elvis taxa* (Erwin and Droser 1993), which evolve after a mass extinction and converge strongly on pre–mass extinction morphotypes, as Elvis impersonators now clutter the landscape, at least if you frequent Las Vegas (so I am told). In Triassic reefs, sponges may be mistaken for Permian taxa, but they are unrelated (Erwin and Droser 1993).

Preservation and rock distributions may strongly bias our perception of geological ranges of taxa. All geological ranges of fossil groups are incomplete, owing to lack of appropriate preserved habitats and poor preservation. As incompleteness, or gaps, between fossil occurrences in a vertical section increases, it stands to reason that the actual temporal range of a taxon is greater than the record would indicate. We thus need a statistical technique to estimate, with some measure of confidence, the likely time period that a taxon lived, before and after its known geological range (Marshall 1995). The number of gaps may also be combined with a fossil recovery potential curve, which might correct for a change in the probability of preservation during the history of the taxa in question (Marshall 1997).

A common change in probability of preservation occurs when a systematic change in rock preservation occurs, as in the reduction of deposition during a regression phase, as at the end of the Permian and just before the end of the Cretaceous. Suppose the ranges of a group of species all ended at the very terminus of the Cretaceous. A gradual reduction of deposition would, by sampling error alone, give the impression of a gradual disappearance of rarer fossil species (Signor and Lipps 1982). This bias has become known as the *Signor–Lipps effect.* Thus, a sudden ending of many taxa can be made to appear gradual merely by a gradual reduction of percent preservation.

Patterns of taxon survivorship of mollusks indicate that mass extinction may or may not be a qualitatively different phenomenon from background extinction. During normal periods, extinctions of mollusks were correlated with planktotrophic larval development and geographic range, whereas clade survivorship was positively correlated with species richness. During the end-Cretaceous event, however, none of these held, and clade survival was correlated only with the geographic extent of the clade. After the event, the correlations found previously again obtained (Jablonski 1986). In the end-Cretaceous extinction of planktonic diatoms, however, a different pattern emerges. Diatom species with benthic resting stages survived far better than those with no resting stages. Foraminifera species with specialized morphologies and larger size were eliminated and simpler morphologies were favored (Keller 1996). Sea urchins suffered extensive extinctions across the Cretaceous-Tertiary (K–T) boundary, but bulk sediment processors and shallow-water herbivorous species suffered more extinction than did omnivores or selective deposit feeders, which suggests a relationship between high extinction and starvation (Smith and Jeffery 1998). Here, properties that normally would be related to survival of individuals can be extrapolated to taxon survival. During the Permian mass extinction, gastropod success did not differ especially from periods of more subdued extinction, but groups with planktotrophic larvae and geographically restricted groups suffered more than average (Erwin 1993). Thus, as extinction intensity increases, some qualitative changes may emerge for some taxa and biogeographic/dispersal properties, but not for all.

Causes of mass extinctions. We discuss below the issue of replacement of ecologically similar forms and whether intergroup competition plays a role in replacement. But there is no doubt that mass extinctions are associated in time with major environmental changes. The problem, of course, is that other times of no mass extinction also mark times of environmental change, and it is fair to say that we could not easily predict all mass extinctions with nonfossil data alone. If environmental forcing, which transcends the abilities of species to survive or adapt, is a major cause of mass extinction, what are the factors? We can list them (Hallam and Wignall 1997), but finding smoking guns is often another matter:

1. Bolide impact or a series of impacts
2. Volcanism
3. Climate change
4. Lowering of sea level: regression
5. Anoxia, especially transgressive spread of deep-anoxic waters onto the continental shelves

These causes are inferred from associations in time between inferred geological events and extinctions, and not from a solid model linking environmental change to extinction. The best example of the latter is the Permian mass extinction. Figure 7.13 illustrates a scenario of environmental change that might have triggered the extinction. The vast marine regression might have been the driving force behind a variety of environmental changes, including a rise in carbon dioxide, which led to increased temperature and oceanic anoxia. At the end of the Permian, sea level dropped, perhaps about 200 meters, which was followed by a transgressive rise of sea level in the Lower Triassic of similar magnitude in just 2 million years. Seasonality and reduction of habitat complexity during the regression may also have

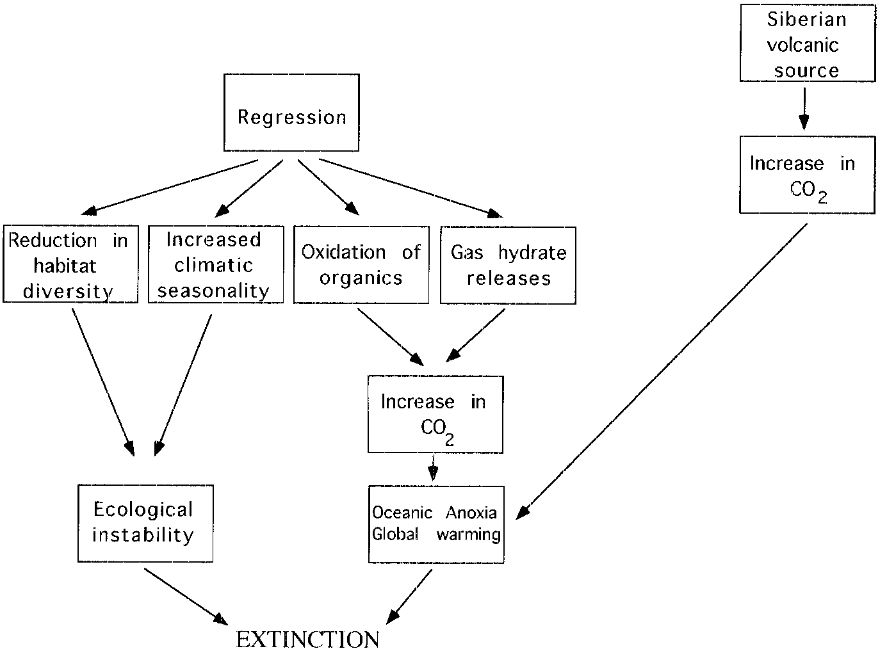

Figure 7.13. Possible contribution of factors to the Permian mass extinction. (Modified from Erwin 1993.)

begotten environmental instability, beyond the adaptive ranges of a number of specialized groups. Volcanism may be a minor contribution to climate change at the end of the Permian, because calculations preclude much of a change in the large ^{13}C deviations at this time, owing to outgassing (Erwin 1993). Doug Erwin likened this multicomponent explanation to *Murder on the Orient Express* by Agatha Christie, where 12 culprits are ultimately found to have conspired to murder the victim. Great for murder mysteries but maddening for science. Even this cast of characters ignores the hypothesis of global cooling triggered by glaciation (Stanley 1988), but this may be discounted, as glacial evidence can be dated much before the extinction begins (Erwin 1993, p. 170). Sea-level change can be implicated in a number of extinctions throughout the Mesozoic (Hallam 1983), but they, too, are often combined with other events, such as bolide impacts.

If it was murder on the Orient Express, can we find the one with the biggest daggar, or the one who stabbed the victim first? Knoll, Bambach, Canfield and Grotzinger (1996) argued that large and seemingly sudden excursions of $^{13}C/^{12}C$ fractionation in the Upper Permian might hold an important clue. Relative increases of ^{13}C in a warm ocean with aggregated continents might reflect active photosynthesis, combined with deposition of carbon into a sluggish and anoxic deep ocean. Carbon would be removed from the atmosphere, reducing greenhouse gases and setting up the world ocean for a cold spell and perhaps an increase in deep water circulation, owing to climatic instability and surface cooling. Relatively sudden and large decreases of ^{13}C might indicate a sudden increase of deep-ocean circulation, which might bring several toxic substances, including carbon dioxide, to the surface, causing mass mortality. These changes would have to be rapid, because over times of a million years or so, carbon equilibration would occur and oceanic fractionation between the surface and the bottom would not occur.

Selective extinction might support this hypothesis, because groups with sluggish body fluid circulation suffer greater extinction, as do groups with greater dependence upon calcium carbonate skeletons. On the other hand, physiologically robust crustacean and molluscan groups would probably survive other environmental insults, such as incursions of anoxic water and increases of H_2S. Also, a transport of CO_2 to the bottom might catastrophically strip nutrients from the shallow ocean, which would also cause extinctions (Martin 1996), although the selectivity would not be explained so clearly. One cannot easily exclude coeval physical events, such as outgassing and particle productions from the Siberian traps (Vermeij and Dorritie 1996). Extraterrestrial gas signatures found recently in boundary-associated fullerenes suggest a possible major impact at the Permo-Triassic boundary (Becker et al. 2001), which might be the great daggar we seek.

The Cretaceous and other mass extinctions: Sudden catastrophe or gradual? The end of the Cretaceous is not the most dramatic mass extinction in the Phanerozoic (Figure 7.4). At the time, however, both major terrestrial and marine elements were lost, the fauna was sufficiently modern to be understood ecologically, and some of our favorites, such as dinosaurs and ammonites, bit the dust. The discovery of a strong positive iridium concentration anomaly in rocks from localities scattered worldwide (Alvarez, Alvarez, Asaro, and Michel 1980; Silver and Schultz 1982) raised the possibility that the extinction might have had an extraterrestrial cause. Both positive evidence (Playford, McLaren, Orth, Gilmore, and Goodfellow 1984) and negative evidence (McGhee, Gilmore, Orth, and Olsen 1984; McGhee, Orth, Quintana, and Gilmore 1986) for an iridium anomaly have been found for the Frasnian–Famennian (Late Devonian) mass extinction, but the extinction itself was spread over at least 7 million years, and climatic effects are evident (McGhee 1982). Solid evidence for impacts postdate the Frasnian–Famennian event (McGhee 1996). There seems to be no iridium anomaly associated with the terminal Ordovician extinction (Orth, Gilmore, Quintana, and Sheehan 1986). A similar iridium anomaly in sediments of 34 million years of age occurs simultaneously with the disappearance of five dominant radiolarian species, and at the general time of a mammalian extinction (Alvarez, Asaro, Michel, and Alvarez 1982; Ganapathy 1982). But the larger picture of biotic change across this boundary is gradual, with no suggestion of a catastrophe (Corliss et al. 1984).

Alvarez et al. (1980) set off a debate that has yet to flag by suggesting that a massive asteroid impact caused the end-Cretaceous extinctions by blanketing the earth with dust spread along ballistic trajectories outside the atmosphere. McLaren (1970) suggested previously that a single impact or supernova could have caused the Frasnian–Famennian extinction. I still remember hearing Digby McLaren's Paleontological Society luncheon presidential address on the subject. I left the room thinking he was crazy and was not alone in this assessment. Well, maybe he was, but we now have the tools to appreciate the wisdom of such craziness!

The fact of an end-Cretaceous impact is supported by the worldwide nature of the anomaly (Silver and Schultz 1982) and by shock structures on quartz crystals (Bohor, Foord, Modreski, and Triplehorn 1984). Impact structures on quartz suggest that an enormous crater should be present on a continent, although other origins for shocked quartz are possible (Carter, Officer, Chesner, and Rose 1986). A wedding ring caused one of the iridium anomalies (or the extinction was caused by a rain of wedding rings), but the other Cretaceous–Tertiary cases withstood further scrutiny (Alvarez et al. 1982; Alvarez, Alvarez, Asaro, and Michel 1984). A possible piece of ejecta has been found in a core of the Pacific at the K–T boundary, which indicates that the bolide was likely a typical metal- and sulphide-rich carbonaceous chondrite rather than deriving from cometary materials (Kyte 1998). The impact has probably been located in the megacrater at Chicxulub in the Yucatán of Mexico (Hildebrand and Penfield 1992; Hildebrand et al. 1993). The crater harbors an armory of smoking guns, including shocked breccia clasts similar to shocked lithic fragments found worldwide, tektitelike glasses, a pronounced iridium anomaly and a ^{40}Ar/^{39}Ar radiometric age from 65.2 million years ago (Koeberl 1993; Sharpton et al. 1992), which match ages of worldwide K–T boundary samples with tektites (Swisher et al. 1992). The crater suggests a bolide of some 10 kilometer in diameter. If the impact were at an angle, presumably more material would be spattered into the atmosphere. Evidence from ^{3}He/^{4}He ratios suggest that the iridium-rich clays may represent no more than 10,000 years, suggesting a catatastrophic extinction for many groups (Mukhopadhyaly, Farley, and Montanari 2001).

Okay, we have an impact, but what are the possible biological consequences? The dust cloud would exist for a time sufficient to severely disrupt climate by cutting off all light, and temperature might have been expected to drop precipitously. A stable oxygen isotope anomaly at the boundary gives evidence for a sudden temperature change. The impact should therefore have affected all organisms dependent on light and warm temperatures. Deep-water forms not so dependent on light or warm temperature, such as nuculid bivalves, would be expected to survive. Alternatively, a hot plume emanating from the impact site could have accelerated the production of nitric acid, causing a worldwide shower of acid rain that might have poisoned the upper ocean (Prinn and Fegley 1987).

The Alvarez theory has one strong prediction and other weaker predictions: (1) extinctions must follow or coincide with the impact; (2) one might also expect many groups to die off instantaneously, but a less catastrophic change in temperature and light might have an effect that would be prolonged; (3) groups more prone to light stress or temperature increase would be more vulnerable (e.g., phytoplankton vs. deep-water deposit-feeding benthos). The response of the sensitive groups should be geologically instantaneous.

How does the K–T fossil evidence stand up? As in most other mass extinctions, the end of the Cretaceous was preferential as to organisms affected. Groups associated strongly (Foraminifera, coccolithophorids) or weakly (ammonites) with the water column suffered the most, whereas benthic forms (e.g., bivalve mollusks) generally suffered less. Members of food webs less dependent on plant material (marine deposit feeders, scavengers, stream inhabitants, and small insectivorous mammals) suffered less than strict herbivores (Sheehan and Hansen 1986). This might argue for a trophic association. I have pointed out, however, that current evidence suggests that deposit feeders depend strongly on the supply of seston from the overlying water to the bottom and could not have lasted much more than a few months longer than those forms that fed directly on phytoplankton (Levinton 1996). The relative success of deposit feeders may be due more to their occurrence in deeper waters.

There is also an apparent temperature-dependent bias in extinction at the K–T boundary: Mollusks and Foraminifera in the tropical Tethys Sea suffered large-scale extinction and were replaced by higher-latitude contemporaries (Stanley 1983, 1984). The question of timing is more confusing. Coccolithophores and nonglobigerinoid foraminifera disappeared so precipitously (and simultaneously with the iridium anomaly) that chalks give way to clastic sediments in a knife-edge contact in several sections. In the chalk of Denmark, the Maastrichtian fauna, dominated by brachiopods, disappears abruptly (Figure 7.14), with no prior warning in terms of reduced diversity, or early extinction of specialized forms (Surlyk and Johansen 1984). The sediments above the chalk are clayey and indicative of anoxic conditions. Turbidity, loss of an appropriate sediment, and anoxia may all have contributed to the abrupt extinction. Radiolitid and hippuritid rudistids bit the dust during a period of flourishing radiation. The current evidence suggests that Cretaceous vertebrates also succumbed at the boundary, but preservation is probably too spotty to tell whether it is sudden in any respect.

Unfortunately, the larger story is not nearly so simple. There is extensive evidence for significant declines in many groups well before the time of the major iridium

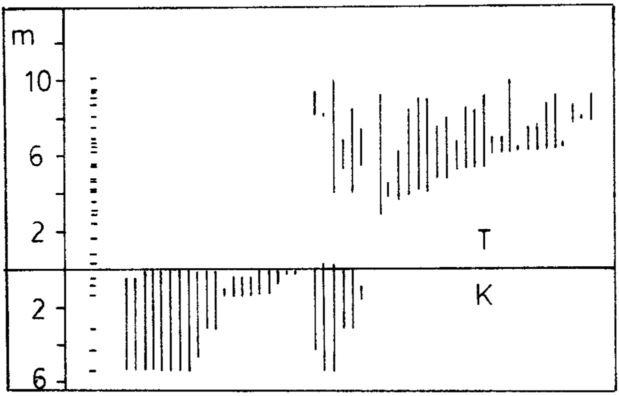

Figure 7.14. Duration chart of brachiopod species in the Cretaceous (K)–Tertiary (T) boundary sequence in Denmark. Note the Lazarus effect: Several species disappear, then reappear after the "extinction." On left, stratigraphic level (meters) and sample horizons are indicated. (After Surlyk and Johansen 1984.)

anomaly, which would falsify the major prediction of the impact hypothesis. Hickey (1981) discussed the record of land plants and concluded that it was compatible with a gradual deterioration of climate. A dramatic change in palynmorphs did occur, however, right at the boundary (Hickey 1984). A gradual deterioration, well below the boundary, seems to be recorded in the record of diversity of the inoceramid bivalves and ammonites (Kauffman 1984). From the Cenomanian to the Maastrichtian stages, there is a continual decrease of the rate of new ammonite generic appearances (Ward and Signor 1983). As Ward and Signor commented, the "diversity faucet" that characterized ammonite evolution was shut down in the Campanian stage, well before the Cretaceous–Tertiary boundary. The story is claimed to be the same for the dinosaurs (Schopf 1982). The dinosaur fauna of the late Maastrichtian included fewer than 20 species in 15 genera and 10 families, chiefly in the North American western interior. There is no good evidence, however, that the dinosaurs were declining steadily toward this low number in the last 9 million years of the Cretaceous (Sheehan and Morse 1986), nor is there a paucity of dinosaur specimens in the time period just before the K–T boundary, as represented by the top of the Hell Creek formation (Sheehan, Fastovsky, Barreto, and Hoffman 2000). One extinction event, that of some rudistids (a group of aberrant bivalves that constructed reefs), was indeed rather brief, but also occurred well before the K–T boundary. In one section in Spain, plankton disappear at the boundary, but two invertebrate groups do not (Ward, Wiedmann, and Mount 1986). Most embarrassing for the impact theory, the freshwater biotas seem to have emerged unscathed.

When sharp, are the disappearances global? If we remove the rudistids, which became extinct earlier, there is no latitudinal difference in Maastrichtian extinction among bivalves (Raup and Jablonski 1993). But earlier bivalve disappearances in the Campanian were concentrated at high southern latitudes, suggesting perhaps the early onset of global cooling that went beyond the thermal limits of many high-latitude species (Zinsmeister and Feldman 1996). Maastrichtian planktonic foraminifera show a dramatic disappearance in middle and low latitudes. At high latitudes, a number of groups survive unscathed into the Danian (Keller 1996). Stable carbon isotopes suggest a drop in productivity in the lower latitude oceans but not at high latitudes (Keller 1996; Zachos and Arthur 1986). Keller (1996) reported that foraminifera were dropping in taxon richness below the boundary and that high-latitude forms survived the K–T crisis; she therefore restricted the crisis to tropical foraminifera.

The sharpness of the boundary for any group is clouded by the imperfections of preservation. If the ranges of certain groups fail to extend all the way to the K–T boundary, then it is possible that perfect preservation would have given us a far different picture. Many western Tethyan ammonites appear to become extinct below the boundary, but Marshall and Ward (1996) demonstrated that the confidence limits of a number of taxa continue right to the K–T boundary. Of course, this does not necessarily prove that the species became extinct at this time; they could have become extinct before or after. The analysis does exclude being sure that the geological range should be read literally. MacLeod (1996) performed a similar analysis with Upper Cretaceous foraminifera and pointed out that the ranges are compatible with a sudden extinction. They also, however, are compatible with many other possible scenarios. Some groups penetrate the boundary, and it appears that there is good evidence that the fossils were not reworked up into the Danian by erosion and bioturbation.

What else was happening at the time? Unfortunately, a lot.

1. In the late Maastrichtian, sea level decreased by 150 to 200 meters, making a hypothesis of increased terrestrial seasonality compatible with the ultimate disappearance. Just below the K–T boundary, sea level suddenly rises.
2. As mentioned above, temperature drops.
3. The Deccan Traps in India, enormous in scope, probably spewed a variety of substances that strongly affected the atmosphere (Officer and Drake 1983; Officer, Hallam, Drake, and Devine 1987; Ray and Pande 1999), and might produce effects resembling those of a bolide impact. But there is solid evidence that the activity predated the K–T boundary (Courtillot et al. 1988; Duncan and Pyle 1988; Venkatesen et al. 1993; Courtillot et al. 2000).

What are we to make of this? Uncomfortable as it may seem, there may be more than one process at work in causing major extinctions. The evidence from land plants (Hickey 1981), dinosaurs, and many mollusks points to a change in conditions well before the K–T boundary. Most notable are groups such as inoceramid bivalves and some of the ammonites that seem to be tracking an environmental deterioration before the termination of the Maastrichtian or final Cretaceous stage (Marshall and Ward 1996). This would violate the fundamental prediction that extraterrestrial events should be followed by, not preceded by, extinctions. But the iridium layer, plus its associated faunal disappearances, cannot be reconciled with any hypothesis of climatic deterioration, unless one could establish a threshold temperature for the production of calcareous plankton. There clearly was a sudden extinction at the K–T boundary, but it was focused on lower-latitude microplankton; we can only speculate about suddenness of extinction in other groups. The Eocene data also suggest a repetition of an extraterrestrial event, perhaps associated with sudden disappearances of radiolarians and other groups. We are left with a compound hypothesis, at least for the proximate cause of the Cretaceous extinctions. Indeed, it may be premature to speak of a Cretaceous mass extinction at all, given the evidence for different and seemingly inconsistent tempos and timings of extinction. Finally, the Deccan traps still haunt the impact hypothesis and the eruptions are even compatible with a strong and sudden change in atmospheric chemistry at the K–T boundary (Ray and Pande 1999).

The same can be said for the Permian extinction. If we believe that sea-level drop was the sole cause, operating by an area effect, we have to reconcile the precipitous change in sea-level coverage in the last stage of the Permian (Schopf 1974), with the pattern of extinction, which was initiated earlier than the sea-level drop (Bretsky 1973). The extinction seemed to concentrate on certain ecological groups, particularly tropical forms at the end, but it affected high-latitude groups earlier in the Permian. Most discouraging of all, what if the extraterrestrial influence occurred in a series of impacts, as has been argued to be possible in the Frasnian–Famennian extinction, rather than as one big bang (McGhee 1996)? Without a series of signals (e.g., a series of definitive iridium spikes of extraterrestrial origin), such a hypothesis is ad hoc at best.

In conclusion, there is credible evidence for an extinction in the end-Cretaceous caused by an impact by an extraterrestrial object or perhaps volcanic impacts on the atmosphere. Although other extinction factors may have been at work in the Late Cretaceous, extinctions occurring before the time corresponding to an extraterrestrial iridium anomaly do not falsify the impact hypothesis. At any time in the record, *some* groups must be declining. Even if we accept the impact as a source of some extinction, the Cretaceous still appears to be a compound event, because environmental change and the pace of extinction both accelerate before the K–T boundary (Jablonski 1997b). Isn't it bad luck that a large asteroid happened to smack into the earth just as sea level was changing as much as it did in the whole of the Phanerozoic? Several other mass extinctions also seem to be complicated and were probably associated with changes in climate and sea level (that are probably interrelated). As Surlyk and Johansen (1984) and Hallam (1984) noted, anoxia may also be an important cause of mass extinctions, as witnessed by the extensive development of black shales in certain periods. What is lacking at present is a credible evaluation of the relative effects of these factors. In the Eocene, low temperature may be the dominant force; it exerted visible effects on organisms, such as leaf morphology (Wolfe and Hopkins 1967). Even here, we cannot exclude a concomitant effect of water column homogenization (Lipps 1970) on the tropical plankton.

Although one can debate forever on the approach of looking for a single cause for a mass extinction, as opposed to multiple causes, it is clear that the biotic consequences are to a large degree similar. However it happened, we lost the trilobites, most of the articulate brachiopods, conodonts, and many other groups by the Early Triassic. By the time of the Paleocene, dinosaurs were gone and land vertebrate communities were completely reorganized as the modern orders of mammals diversified. Reef decimation at the end of the Permian and Cretaceous caused major changes afterward. The mass extinctions resulted in major taxonomic and ecological reorganization.

Mass extinctions: Recovery and opportunity? Imagine the world following the Permian extinction. Over 95% of the ocean's marine species were probably gone, over half the families were extinct, organismal abundance was low, and major loci of biodiversity, such as calcareous reefs, were missing entirely. The rich biotas of the chalks of the Upper Cretaceous give way to miserable biologically sparse clays. After the Permian lowering of sea level, a sudden rise in sea level in the Early Triassic might have brought anoxic deeper waters onto the earth's shelves, adding global catastrophe to Armageddon (Wignall and Hallam 1992). Even the survivors might have been extremely rare or at least confined to small enclaves.

Some rules of extinction and recovery do apply (Erwin 1998):

1. Mass extinctions usually selectively favored the survival of ecological generalists.
2. Specialists and large-bodied species faced increased extinction.
3. Reefs were especially vulnerable to mass extinction, and recovery was prolonged or nonexistent.
4. Lower-latitude biotas might have been less able to withstand sudden environmental change (but see Raup and Jablonski 1993), although global cooling might have clipped off higher-latitude forms.
5. Survivors often appeared after a geological section that is relatively barren of fossils. Survivors usually were small in body size, were geographically widespread, and often formed dense fossil layers, reflecting opportunistic dispersal and recruitment events (Levinton 1970).

During the period just after the extinction, there perhaps was an interesting opportunity for expansion and adaptive diversification of species formerly rare, or even newly appearing. In many cases, these opportunities are taken up apparently by generalist taxa that survive the extinction and are of small body size and generalized morphology. The planktonic foraminifera radiating following the K–T and end-Eocene extinctions consisted of species with generalized morphologies and relatively small body size (Cifelli 1969). Alternatively, species well adapted to the stressful environmental conditions during the mass extinction might have had the opportunity to expand. Such *crisis progenitor species* usually lived in the areas most affected by the extinction (Kauffman 1996). The Cenomanian–Turonian (Upper Cretaceous) extinction involved at least a major anoxia event in deeper offshore waters and perhaps an incursion of anoxic waters onto the shelves, killing a substantial proportion of the rudistid bivalves. Inoceramids, a group of semi-infaunal bivalves that dominated Cenomanian outer shelf tropic soft sediments, were particularly hard hit, but the early Turonian was marked by the radiation of another inoceramid group, the genus *Mytiloides* (Figure 7.15), which had formerly occupied stressful shelf microhabitats (Kauffman 1996). Three lineages survived the boundary and one radiated in the early Turonian. By contrast, species of *Inoceramus* were adapted to more sta-

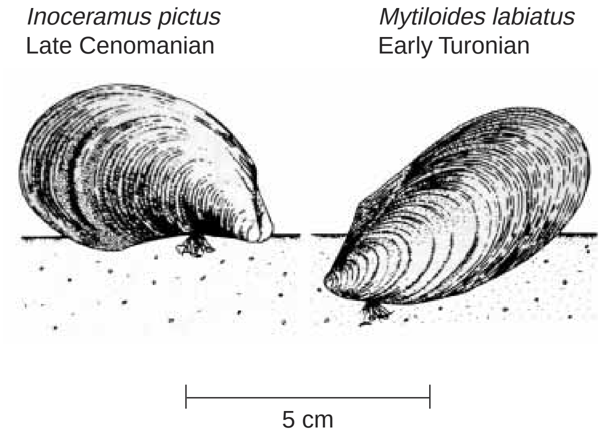

Figure 7.15. Dominant inoceramids before (*Inoceramus pictus*) and after (*Mytiloides labiatus*) the Cenomanian–Turonian extinction boundary. (After Hallam and Wignall 1997.)

ble and less stressful environments and laid low during the early Turonian but radiated extensively later in the mid-Turonian when more benign environments returned to the outer shelves. *Mytiloides* became rare at this time but survived in low abundance to seed other later radiations when environments similar to those of the Cenomanian–Turonian returned. Thus, in effect, the crisis progenitor group was piggybacking the equilibrium species assemblage in good times, but the reverse was true in bad anoxic times.

If generalists survive mass extinctions, then we can see immediately that a crucial aspect of living communities may be sundered and that is the web of specialist dependencies, such as mutualisms, specialized animal–plant host interactions, specialized predator–prey interactions, and the like. This would suggest that an entire new set of dependencies should evolve, but it is not clear whether this would slow down the reestablishment of a diverse community. Indeed, we do not have an estimate of how extinctions of the so-called interdependent component of a biota would cause a long-lasting and perhaps unrecoverable damage to a community. This problem applies not only to the largest mass extinctions but even to the small-scale extinctions that are observed commonly throughout the record.

As we attempt to place a magnifying glass on the effects of extinctions, we immediately encounter the conundrum of the molecular dates of major divergences, which commonly predate major radiations following extinctions or during major environmental changes. For example, radiations of continental songbird lineages were believed to be associated with rapid changes imposed by the periodic Pleistocene glacial advances and retreats, but molecular clock dating suggests a relatively protracted time of divergence of North American songbirds over the past 5 million years. Despite fossil evidence of the earliest appearance of modern mammal orders in the Paleocene (e.g., Alroy 1999), two molecular estimates place the divergence of the eutherian mammals well before the K–T boundary (Hedges, Parker, Sibley, and Kumar 1996), as if the fossil record of the Cretaceous is somehow hiding these groups, perhaps owing to misidentification or lack of preservation of the geographic locus of evolution of these groups. A similar story has emerged for birds (Cooper and Penny 1997; Hedges et al. 1996), which leads to the strange notion of mass survival of groups across the K–T boundary, because they were there already, at least by molecular inference (Cooper and Penny 1997). O'Brien, Menotti-Raymond, and Murphy (1999) added a sophisticated brew of molecular data, including chromosomal rearrangements and fusions, which are relatively conservative characters conducive to useful phylogeny construction. Although still at a comparatively early stage of development, data on chromosomal rearrangements place the primate–carnivore split at 80 million years ago, well before their appearances as fossils.

Taken at face value, the molecular evidence points to a striking problem with fossil data. It is possible that in the early stages of radiations, the groups might have been morphologically similar, ancestral in appearance, and lacking the autapomorphies that might allow us to identify the eutherian groups. Alroy (1999) noted that the Upper Cretaceous contained a very small number of mammal species, which multiplies to a large number in the early Cenozoic. He argued, therefore, that this is the signature of an evolutionary radiation. However, if the eutherian phylogenetic splits occurred before the Upper Cretaceous, it is unlikely that extinction would eliminate all of the member species of all of the groups, simply because one has to drive all member species of a group to extinction to eliminate the larger taxon. There thus may be a disparity between the appearance of the identifiable groups in the fossil record and the divergence times (Norell 1992). This may mean that there is often a storehouse of evolutionary material, at the ready when an ecological vacuum appears. It also may mean that there is something wrong with the molecular dates. Perhaps there is an acceleration of DNA substitution rate during radiations, which makes the clock tick faster. If this were so, the molecular dates calibrated on other times would overestimate the time of radiation.

Paleontologists have a lot at stake in these arguments. After all, if the divergences arise before they are readily seen in the fossil record, how do we really know what characters were involved in the evolution of crown groups? Further, what are we missing? On the other hand, molecular proponents are left equally in a corner. If the divergences of the modern mammalian orders really do occur after the start of the Paleocene, then what is wrong with the molecular clock estimates? Indeed, this argument spills over to the debate over the Cambrian explosion, which is discussed in chapter 8.

One of the most intriguing points made by paleontologists turns around a simple calculation of the probability of missing pre-Paleocene fossils that would lead us to think that the molecular divergence estimates are not correct. Foote, Hunter, Janis, and Sepkoski (1999) used measurements of rates of origination, extinction, and preservation to extrapolate backward to see if the absence of Cretaceous fossils of modern orders made quantitative sense. Preservation rate arises from an estimate of the percent of species durations that are recorded; a low preservation rate, combined with high extinction rate, makes it less probable that we will find a lineage in the fossil record. Foote and others have pointed out that a missing record (some 64 million years) implied by molecular estimates suggests absurdly low preservation rates, given our knowledge of the record of mammalian fossils. Although this sounds really good for the veracity of the fossil record, it is still possible (1) that an unexplored region may have the ancestors, given a lack of Upper Cretaceous mammal-bearing deposits on three continents, and (2) that the fossils are right in front of our eyes but have been overlooked. Given the recent discoveries of Precambrian embryos, Lower Cambrian fossil fish, and so on, these are not exactly points to be overlooked.

Archibald (1996) affirms the monophyly of the major crown groups of Cenozoic mammals but points out that a superordinal grouping of ungulate mammals are linked to 85-million-year-old Late Cretaceous mammals. A group known as zhelestids form a group of stem taxa that can be related to early Tertiary condylarths, which in turn can be related to a number of placental mammalian orders (Archibald 1999). Uncontested Eutherians can be found in the earliest Cretaceous, which makes a story of early divergence very credible. The presence of a number of Eutherian groups in the Cretaceous suggests that splitting was already underway (Hedges and Kumar 1999). What is not clear is the character of the groups that might have split in the Cretaceous. They may represent a series of stem groups that lack the distinct apomorphic features of the crown ordinal groups of eutherian mammals.

Extinction and opportunity: Hypotheses of competitive elimination and clean sweeps. Darwin worried much about extinction, particularly because there was much evidence in his time that some of the "races" of humankind had disappeared. It is said that Alexander Humboldt heard a South American parrot who was the last creature capable of speaking the words of a lost tribe. The forces of civilization were causing widespread decreases of aboriginal peoples throughout the world. Darwin (1859) viewed the survival of any species during normal times as a delicate balance that could be easily upset. Many factors, including disease and climate, could tip the balance toward population decline and extinction. He saw the influx of western humankind as a small but crucial factor in extinction, as "each race is constantly checked in various ways; so that if any new check, even a slight one, be superadded, the race will surely decrease in number; and decreasing numbers will surely lead to extinction" (Darwin 1872, p. 208). The notion of plenitude led Darwin to believe that competitive superiority was the source of extinction. This stemmed directly from the notion of the tangled bank, where plants and animals filled every nook and cranny. But could the tangled bank be extrapolated to global catastrophe?

An alternative point of view springs immediately from the record of replacements often seen in the fossil record and especially the record of recovery following mass extinctions. Major disruptions of habitat might have swept the world free of many taxa; subsequent replacements and expansions are therefore the result of happenstance and opportunity. This point of view is inconsistent with a common belief that successful survival of extinctions is always influenced by competitive superiority – that is, a belief that the adaptively "better" forms survive and proliferate, after eliminating a competitively inferior group. We can't exclude this hypothesis, but current evidence provides no general confirmation of it. In a large analysis of potential for competitive replacement among tetrapods, Benton (1996) concluded that potential for competitive replacement was uncommon. Sessile colonial benthic invertebrates such as bryozoa are commonly space limited (Jackson 1979), but even here, the evidence for competitive interactions in macroevolution is unconvincing. The cheilostomes generally overcome cyclostomes in competitive bouts in living faunas, but when the cheilostomes radiated through the Cretaceous and Paleogene, there is no evidence that the cyclostomes were affected very much. During this time, the cyclostomes increased to a plateau and did not decline (Lidgard, McKinney, and Taylor 1993).

Recovery from mass extinctions suggests the creation of an ecological void, followed by invasions of ecological opportunists, which are eventually followed by an evolutionary radiation. It may be that the rate and magnitude of the environmental crisis may influence whether species can adapt to the change, but there is no convincing evidence that distinguishes between such so-called *press extinctions* and *pulse extinctions,* which ravage any potential for adaptive response. As mentioned above, pulse extinctions, like the end-Cretaceous extinction, may or may not be selective with regard to ecological properties of individuals that might confer increased survival. As mentioned above, evidence supporting coordinated stasis might argue for press extinction, but so far there is no compelling theory or data that support accepting it.

We have not discussed one of the major phenomena characteristic of many extinctions: replacement by ecologically similar forms. This is hard to document because of the common problem of devising criteria for ecological similarity. We are here at the interface of ecology and evolution, as groups that are sparse before a mass extinction may change significantly in ecology and morphology via evolutionary change to effectively replace another group that disappears. The mammals seem to have been mainly minor and nocturnal elements of the terrestrial fauna until the disappearance of the dinosaurs and other reptiles. (There were, however, more mammal genera than dinosaur genera at the close of the Cretaceous.) Subsequently, in the Paleocene and Eocene a major radiation resulted in mammalian replacement of ecological space occupied formerly by the dinosaurs. But this replacement is hard to draw in any detail. How, then, do we draw an ecological equivalence between Mesozoic mammals and dinosaurs?

This problem appears in two alternative hypotheses explaining replacement: (1) The *competitive displacement model* argues that once a competitively superior group arises, it displaces its contemporaries, (2) alternatively, the *vacancy hypothesis* would argue that after one major ecological group disappears, another takes its place. The second hypothesis could operate in two distinct ways. One group may not be inherently superior (e.g., larger mammals over dinosaurs), but its rise is suppressed simply by the temporal priority achieved by an extant and wide-ranging group. Thus, the larger mammals might not have been able to "get off the ground" without a minimum available area and habitat complexity for expansion, which appeared only after the end of the Cretaceous. Alternatively, following extinction of one group, a second that has survived a crisis may simply expand randomly to fill the place of the first.

The competitive displacement model may apply in some cases. Thayer has carefully classified much of the fossil benthic invertebrates into ecological functional groups, making resource use comparisons possible. The pedunculate brachiopods, for example, decline from the Devonian toward the end of the Paleozoic; this coincides with the expansion of their ecological equivalent, the epibyssate bivalves (Thayer 1983). But many of the large-scale replacements recorded in the fossil record seem to involve disappearances, followed by radiations of either the same group (e.g., Foraminifera: Cifelli 1969; trilobites: Palmer 1984) or quite different groups of organisms (e.g., mammals replacing dinosaurs). The reclining brachiopods decrease precipitously at the end of the Permian; this is followed by a great diversification of free-burrowing bivalves in the Mesozoic. Thayer has documented (Figure 7.16) a major increase in bioturbation during the Mesozoic. It is reasonable to believe that this revolution prevented the reexpansion of the free-lying brachiopods into these habitats.

Unfortunately, replacements are difficult to document, and evidence can be interpreted differently. The brachiopod–bivalve switch in dominance from Paleozoic to Mesozoic is a case in point. Gould and Calloway (1980) examined diversity changes of both groups and found a general positive correlation between the two in degree of change of taxon richness, following the Permian extinction. This was taken as evidence that the two groups could not have influenced each other negatively. Thayer (1983) has criticized this conclusion, noting that Gould and Calloway did not take functional groups (groups with ecological equivalence) into account. At the level examined by Gould and Calloway, the positive correlation may just involve overall indications of the "health" of the world biota, or even worse, correlations between poorly preserved and well-preserved fossil biotas, when both groups are well, or poorly, preserved. The emphasis on diversity may also be deceiving, as it does not take abundance into account. Taxon richness of pedunculate brachiopods did not decrease very much after the Permian, but individual abundance changed

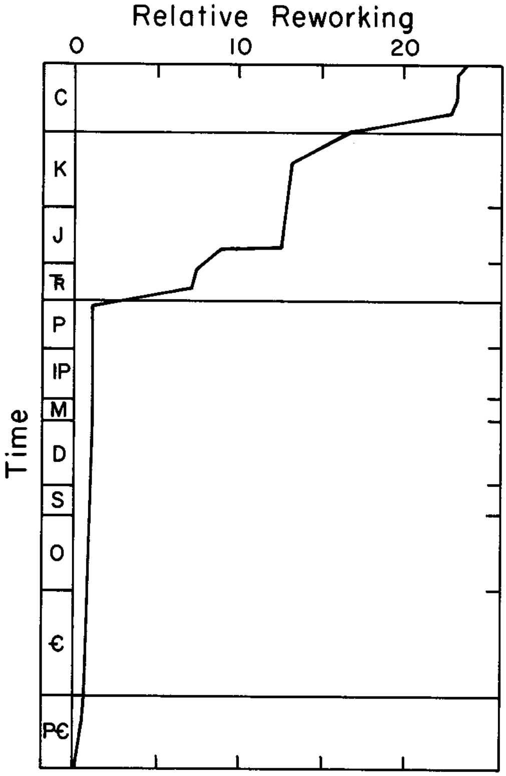

Figure 7.16. Estimate of relative amounts of biogenic reworking of shelf sediments through the Phanerozoic. (After Thayer 1983.)

considerably, relative to the Pennsylvanian and Permian (Thayer 1983). The post-Permian, quite simply, was no longer a brachiopod world.

The question of individual abundance versus taxon richness can also be considered at the community level. Bivalve-dominated faunas may often be species-poor yet may dominate by virtue of their competitive ability. In faunas of the northwest United States, two conspicuous communities demonstrate this. Subtidal mud bottoms are often completely dominated by a single mytilid (Mollusca, Bivalvia) species, *Modiolus modiolus,* whereas several brachiopod species exist as relatively minor components. In very shallow subtidal and low intertidal habitats, succession usually leads to dominance by *Mytilus californianus,* but several species of brachiopods can also be found, though they are usually rare and in apparent refuges.

Sepkoski (1996) used an updated brachiopod–bivalve database to reexamine Gould and Calloway's results and interpretation. Most importantly, he noted that the use of linear regression on Paleozoic brachiopods is invalid, because there is an obvious pattern of increase, peak, and decline of diversity. This suggests that any interactions between bivalves and brachiopods might involve nonlinear effects, which he modeled using the logistic equation. He argued that, yes, the Permian is an obvious interruption, but one can use a simple coupled logistic model (where the upper limit, *k,* is an upper limit on number of species) to predict the success of the bivalves and the demise of the brachiopods. The apparent steady decline of brachiopods in the Mesozoic occurs while the bivalves are steadily on the rise, which supports the simplest competitive model of gradual replacement. Although the modeling match is successful, unfortunately there is no basis for the parameterization of the couple logistic beyond curve fitting, so more is needed here to resolve the problem.

Competition and evolutionary responses of competitors are difficult to document, except in living communities, where experimental approaches are possible (Schoener 1983). Evidence for the direct effects of one group on the evolution of another comes more easily in studies of predation. There is extensive evidence for a major Mesozoic–Cenozoic evolution of victims in response to the rise of many groups of predators, principally decapods and teleost fishes (Vermeij 1977). The best case is for the gastropods. Forms with morphological characteristics indicative of protection against shell crushing have increased since the Cretaceous. The proportion of umbilicate and trochiform species remained high and relatively constant from the Silurian to the Early Triassic. The overall aspect of the gastropods changed radically starting in the mid-Mesozoic; groups with thickened or expanded adult outer lips diversified, even though the form type had appeared earlier in the Paleozoic (Vermeij 1983). The association with the rise of predators is very suggestive. The same traits appeared independently in many taxa, making an individual adaptation hypothesis, rather than a species culling hypothesis, more likely. This trend is also concordant with a temporal increase in frequency of shell repair, presumably as a response to predators, from the Paleozoic to the post-Paleozoic (Vermeij, Schindel, and Zipser 1981). Dietl, Alexander, and Bien (2000) documented a temporal escalation of apparent predation on bivalves on a smaller timescale between the Late Cretaceous and early Paleocene. The patterns seen in the fossil record can also be recorded in Recent distributions. Gastropods with features conferring resistance to shell crushing are found generally in areas where robust decapods are common (Vermeij 1977).

Some similar trends may have occurred in other taxa. Palmer (1982) documented a reduction in numbers of parietal plates in seven of the eight families of balanomorph barnacles. All four species of the drilling gastropod *Thais* on the Pacific American coast selectively attack barnacles on the margins of the parietal (lateral) and opercular plates. The trend in plate reduction occurred coincidentally with the radiation of muricacean gastropods starting in the Late Cretaceous, and the one balanomorph lineage evolving free of this pressure maintained the primitive condition of eight plates; this group lives on the integuments of marine reptiles and mammals. The minimum number of four parietals is set by the need to expand the size of the aperture with increasing growth.

In conclusion, replacement and responses to biological challenge are distinctly nonrandom processes, but the mechanisms are not always clear. In most cases of potentially competing groups, extinction seems to have preceded replacement. Here, the possible resolution power of competitive hypotheses is very weak, because it is not clear how we would prove, for example, that the group that finally wins out happened to be suppressed (e.g., Mesozoic mammals) during the period that the prior group (e.g., dinosaurs) dominated. The failure of new novelties to arise in the mammals would be an ad hoc hypothesis immune to test. In cases of gradual replacement, Thayer's use of functional groups has greatly improved our perception of trends in the bivalve replacement of the brachiopods, but there is still the nagging uncertainty that the two groups really were "ships passing in the night," as characterized by Gould and Calloway (1980). The failure of a group to reradiate is more interesting. The nonpedunculate brachiopods failed at this in the early Mesozoic; this is at least coincidental with the takeover of their preferred habitats by bioturbators.

At the end of the Permian, the Paleozoic EF suffered far more than the Modern EF. This may relate to the dominance of the Paleozoic EF by forms reliant on warmer habitats. Once extinguished, the Paleozoic EF reradiated in both the Triassic and Jurassic more rapidly at first than did the Modern EF. Yet it failed to take over despite its apparent increased rate of cladogenesis. It has been consistently more prone to extinction, despite its higher rate of cladogenesis (Sepkoski 1984). This at once suggests that sheer speciation rate (inferred from family appearance rate) is not the key to success, but it also suggests that the ascendancy of the Modern EF could not have been entirely due to their competitive superiority for limited resources. The ascendancy of the Modern EF may have been due to, for example, their coincidental origin in areas with colder climate or relative adaptability to cold; the Paleozoic fauna might have been filtered out by causes extraneous to their potential competitive interactions with other groups. But given their presence after the Permian and Upper Triassic extinctions, it is possible that the surviving groups were facing increasingly stiff competition or predation. This may be reflected in Sepkoski's observation that the Paleozoic EF finally began a slow decline in the Cretaceous after the total number of families exceeded the Paleozoic "steady state." At this point of possible saturation, true competitive decline might have been caused by the Modern EF. This same trend can be seen in the mid-Paleozoic, when the rise of the Modern EF reached the point that saturation was surpassed; from that time on, the Paleozoic EF declined. A functional group analysis would clarify whether this reciprocal change in taxon richness might have been related to competitive interactions.

In chapter 1, I supported the argument (Eldredge 1982; Gould 1982a, 1982c; Levins 1970; Lewontin 1970; Valentine 1968, 1969; Vrba and Eldredge 1984) that many evolutionary processes are hierarchical. Mass extinction exhibits this major feature of evolution (Jablonski 1986). At both ecological and taxonomic levels, the effects of extinction often are reflected at hierarchical levels higher than that of the individual. The explanations vary from area covered by a taxon to ecological properties of individual organisms (e.g., dependence on light or water column structure). By extinguishing groups at high taxonomic levels, extinction of a family would of necessity affect properties at lower levels of the hierarchy, simply because a given feature of a given group happened to "be there" when a catastrophe occurred. Thus, disasters that affected Permian reclining epibenthic marine organisms because of their overwhelming presence in tropical communities (Stanley 1984) might be due to cold temperature affecting the entire tropical habitat rather than to the individual adaptations for reclining.

This conclusion is in no sense antithetical to the Modern Synthesis. Adaptation confers success in a given habitat, under particular ecological circumstances – no more. It's therefore a lame argument that, for example, "the first clam that fused its mantle margins or retained its byssus to adulthood may have gained a conventional adaptive benefit to its local environment. But it surely didn't know that its invention would set the stage for future increases in diversity" (Gould and Calloway 1980, p. 395). The potential for the future is irrelevant to the adaptation (e.g., Mayr 1983). The statement that "many features must come to prominence through their fortuitous phyletic link with high speciation rates" (Gould 1982a) is more a complementary notion than a complete reformulation of evolutionary theory, which Gould admitted.

The adaptations required to resist processes that operate at larger taxonomic levels often have little or nothing to do with those that operate at lower ones, even if the reason for extinction resistance can stem from the same level of the hierarchy. A clear example is mass extinction. Genetic variation in temperature resistance is a common feature of marine invertebrates, showing within-species and between-species variation. Drilling by naticid gastropods is a feature that facilitates prey capture and also could presumably evolve from within-species variation. If the extinction of many groups was due to cold temperature, as claimed by Stanley, then the former adaptation, easily constructed from standard genic variation, is the relevant consideration, not the latter feeding adaptation. At the extreme, which I would not support, one might argue that all of the species dying out during an excessive cold event were those simply lacking adaptations to cold temperature, irrespective of whether 1 or 100 taxonomic families disappeared. All properties of lower levels (e.g., shell sculpture) would therefore be carried along. This is a destructive rather than a constructive process. If the evidence from predation is any indication, most progressive evolutionary trends are constructive and probably are dominated by phyletic evolution, as well as by spurts of success that result from key adaptations.

Can extinctions be titrated? The evidence on extinction depresses us into realizing that we have no formula that can relate a degree of environmental change to percent extinction. Consider the relationship between shallow-sea coverage of the continents and Mesozoic extinction (Hallam 1983; Figure 7.17). Areal coverage of continents declines at the end of the Norian (Upper Triassic), Jurassic, and Cretaceous. More ammonite genera disappear in the Norian, when the sea-level decline was the least, and the group nearly becomes extinct as it did at the end of the Maastrichtian. We find much greater difficulty in making comparisons between other extinctions. Not much change in continental coverage occurred during the Pleistocene and total extinction was modest (Wise and Schopf 1981). Loss of continental coverage by shallow seas is far greater at the end of the Permian and far more taxonomic families and species were lost, but do we have a predictive scale to connect sea-level change to extinction on a finer scale? I would contend that we do not. After all, an apparent climatic deterioration leading up to the Pleistocene resulted in a large-scale extinction and an equal rebound of tropical Atlantic American invertebrates (Jackson, Jung, Coates, and Collins 1993), but it is not clear that the deterioration was of large magnitude.

Of course, the greatest opportunity to develop a titration curve for extinctions comes from a range of volcanic eruptions or extraterrestrial impact intensities (Raup

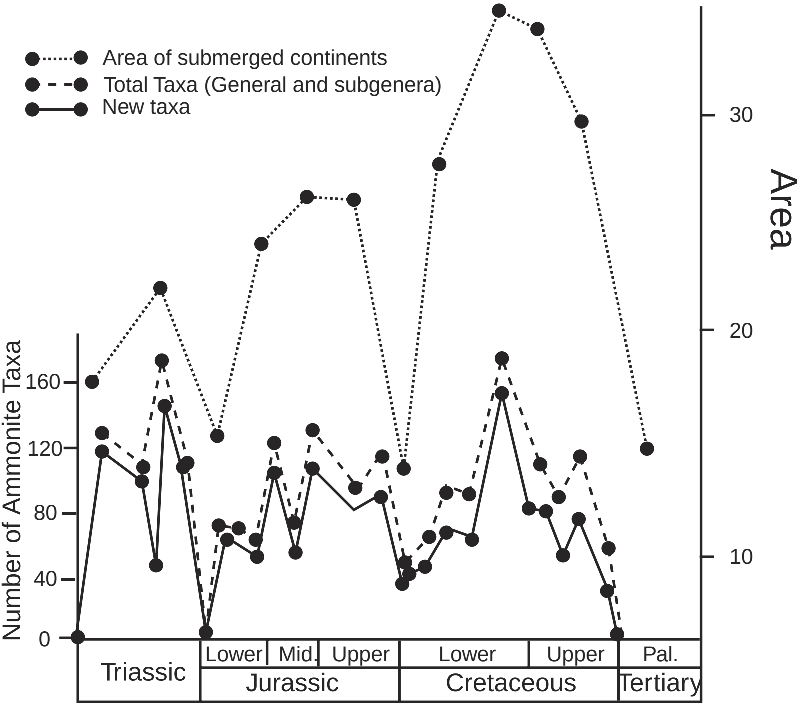

Figure 7.17. Mesozoic to early Cenozoic relationship between ammonite genera and subgenera and area of continents covered by sea, which presumably is correlated with sea level. Note that the smallest change in area covered resulted in the largest extinction. (After Hallam 1983.)

1991b). I link these two types of events because of their similar possibilities of causing global atmospheric change in temperature, acid rain, and so on. On the smallest scale, we can think of the recent eruption at Montserrat in the mid-1990s. Acid rain and volcanics destroyed much of the cloud forest and ash smothered some of the adjacent coral reefs. Corals and sponges were smothered and survivors were bleached (D. Brosnan, personal communication 1997). On a larger scale, the great Krakatoa eruption spewed ash that covered the world and was responsible for the cold year of 1883. Now, what is the relationship between such small events that might have caused extinction of local endemics and worldwide events such as the Cretaceous? This question is obviously rhetorical. Worse than that, do we really know that larger impacts and episodes of volcanism caused more extinction? Frustration rises to a boil again when you realize that the two greatest episodes of volcanism occurred at the end of the Permian and the end-Cretaceous, when similarly record-breaking changes in sea level were occurring, not to mention that likely asteroid that hit at the K–T boundary. High levels of volcanism are also associated with the Eocene–Oligocene series of extinctions, which has been associated poorly with impacts (Hut et al. 1987) and global cooling (Hansen 1987; Kennett et al. 1985). Worse than this, are there events of these magnitudes that caused no extinction? Well yes, maybe. The 45-kilometer-wide early Eocene crater on the Nova Scotia shelf is searching for an extinction (Jansa, Aubrey, Gradstein 1990), as is a large Miocene crater in Bavaria (Heissig 1986). A depression some 250 kilometers in diameter and 850 kilometers deep in Antarctica has the morphology of an impact crater and is associated perhaps with the australite tektite-strewn fields of Australia (Weihaupt 1976). If this were an impact site, we would expect that the bolide were some 25 kilometers in diameter and, if related to the Australian tektites, would be Cenozoic in age.

Anoxia appears associated with a number of mass extinctions (e.g., Hallam 1989). Especially in the Paleozoic, there is widespread evidence for basinwide deeper anoxic waters, as evidenced by widespread black shales that are not bioturbated (Berry and Wilde 1978). Destabilization of stratified oceans, perhaps accompanied by transgression, might have brought anoxic waters onto the shelves, causing major extinctions (Wilde and Berry 1984). The end-Permian extinction might have been caused by or exacerbated by a transgression of anoxic deeper waters, as mentioned above. But anoxic events are common in the fossil record, and it is not clear that all have caused major extinctions. Species requiring oxygen might have been able to survive in refuges on the shallow shelf. A number of Cretaceous anoxic events appear to have no associated mass extinctions (E. G. Kauffman, cited in Erwin 1993, p. 244). In the last few tens of millions of years, the deep ocean was probably oxygenated, save for a persistent oxygen minimum layer to be found in the Pacific and elsewhere. Such a configuration makes it unlikely that the transgressive-anoxic mechanism has universal application to extinctions.

Context therefore appears to be required before one can begin to understand extinction and mass extinction. What is major in some times may be truly unusual in others. Indeed, even the most pervasive theory of extinctions, the impact-periodicity theory, works only if one looks for peaks in extinction against the local background extinction for each event. The mid-Miocene extinction event required by the 26-million-year periodicity hypothesis consists of only five families, but Mesozoic extinction events are typically of much greater magnitude (Hoffman 1985, 1989b). This may mean either that the forcing event was more benign or that the fauna was more resistant to extinction, but it certainly defies us to produce an environmental change–extinction titration function.

Periodicity in extinction, or just ups and downs? The presence of clear peaks in turnover and extinction do not suggest pervasive solutions to the study of the causes of extinction. Many changes in the earth's history are plausible sources of extinction, and some major processes such as sea-floor spreading and continental drift might have had impact on climatic, dispersal, and area effects simultaneously. Although area effects can be invoked in predicting the magnitude of extinctions (Permian vs. Pleistocene), too often we would not be able to "predict" an extinction with paleogeographical, lithostratigraphic, or lithological evidence alone. Episodes of large-scale volcanism, for example, might have caused decreases in earth surface temperature sufficient to cause extinctions, but no such event can be characterized well enough to predict the occurrence of an extinction; we are left with correlations. Although Schindewolf (1950) was once alone, and ridiculed, in proclaiming that unique extraterrestrial events caused major extinctions, we are still left only with firm evidence at the end-Cretaceous, despite the presence of a larger chorus of supporters of other alien bombardments.

Periodicity of extinction or climatic change predicted by astronomical or geophysical theories would be the most convincing way to establish a terrestrial or extraterrestrial cause of extinction. If extinctions are measurably periodic, it may be that only one credible cyclic theory would fit the available pattern. The precedent for such an approach lies with the long-standing debates over the periodicity of Pleistocene glaciations. The Yugoslav astronomer Milankovitch (Hayes, Imbrie, and Shackleton 1976; Imbrie and Imbrie 1979) suggested, following earlier nineteenth-century conjectures, that Pleistocene glacial advances and retreats might be regulated by changes in high latitude insolation, caused by cyclic changes in the earth's orbital eccentricity, tilt, and time of perihelion. A power spectrum analysis of temporal changes of abundance of planktonic fossils in oceanic cores corresponded well to climate changes estimated by stable oxygen isotopes and to periodicity peaks predicted by the Milankovitch theory (Imbrie and Kipp 1969).

A number of studies in recent years have taken up this theme and related these cycles to sedimentary cycles, including some of the classic midcontinent alternations of carbonate and mudstone. Many of these cycles occurred during times when there was no significant amount of continental glaciation, and they represent transgressive–regressive cycles. For example, sedimentary cycles in the lacustrine Early Mesozoic supergroup correspond to periodicities of approximately 25,000, 44,000, 100,000, 130,000, and 400,000 years. These periodicities, in turn, correspond to those expected from celestial processes, such as the precession of the equinoxes, the obliquity cycle, and the eccentricity cycle (Olsen 1986). Cyclic processes such as the precession of the equinoxes may have driven continental heating cycles that rearranged wind and climate. A cyclicity in precipitation would explain the lacustrine sedimentary cycles reported by Olsen.

Milankovitch climatic rhythms also appear in mid-Cretaceous black shale sedimentary cycles in central Italy (Herbert and Fischer 1986). These cycles consist of alternations of carbonate and shale, with intervals of highly oxidized (red) and highly reduced (black) strata. They are particularly interesting because they occur in marine sequences and must have reflected periods of ocean bottom anoxia, alternating with vigorous bottom mixing and high productivity in the water column. This suggests temporal swings in climate that were forced by celestial processes. Salinity and temperature variations may be the link between the external forcing and anoxic–oxic cycles. Milankovitch cycles may also explain rearrangements of southern hemisphere oceanic currents that allowed dispersal into an otherwise isolated Antarctic marine fauna (Clarke and Crame 1992). On an even smaller scale, E1 Niño–La Niña cycles and North Atlantic oscillation cycles impose cycles of primary production, toxic phytoplankton, and benthic abundance in small bays and fjords, such as the Swedish Gullmar Fjord (Belgrano, Lindahl, and Hernroth 1999; Lindahl, Belgrano, and Davidson 1998).

These results may be crucial to our understanding of evolution, because these cycles occur well within the timescales of speciation for many invertebrate groups (see Stanley 1979). Because these cycles reflect both alternations of sediment type and water quality, neither the plankton nor the benthos are immune. Such cycles may set the pace of morphological evolution and may even create periodically reversing directional selection. If the proximate effects of these cycles are long periods of stable climate, interrupted by rapid switches, then we may have a primary driving force for punctuational character evolution. On the other hand, if such cycles create continual gradual change, then directional selection may be continuous and cause a steady response in certain traits. The interested reader should consult Herbert and Fischer (1986) for a summary of Milankovitch cycles.

The earth's history has been dominated by large-scale changes in climate, arrangement of continents, volcanism, and sea level. Fischer (1984) developed a theory connecting physical conditions with the overall pattern of Phanerozoic life. Two summaries (Hallam 1977b; Vail, Mitchum, and Thompson 1977) of global sea-level change show distinct highs in both the mid-Paleozoic and Mesozoic. Periods of continental breakup, when dispersed and thinner continents resulted in smaller ocean basins, would be associated with higher sea levels. Periods of continental aggregation, when continental crust was bunched up owing to collisions and ocean basins were therefore more commodious, resulted in lower stands of sea level. The temporal variation in granite emplacement matches the sea-level curve. This suggests a causal link between active continental fragmentation, volcanism, and sea level, an environmental condition of obvious importance to the world marine biota.

Vermeij (1995) proposed a related hypothesis relating emplacement of volcanic rocks to nutrient supply, which, in turn might subsidize the diversification of early Paleozoic life. Unfortunately we have no algorithm to relate nutrient supply to degree of volcanism, but Vermeij's hypothesis may still be potentially interesting. Following John Martin's visionary research (Martin 1990; Martin and Fitzwater 1988), it has been discovered that phytoplankton production in large sections of the ocean is limited by iron (discussed well in Falkowski, Barber, and Smetacek 1998). A large-scale iron enrichment experiment in the eastern equatorial Pacific resulted in an enormous increase of phytoplankton, which suggests that deposition of iron-bearing dust may cause sharp increases in oceanic production (Behrenfield, Bale, Kolber, Aiken, and Falkowski 1996). Such a dust supply is unavailable now, except in the wind shadow of places such as North Africa. Increases in iron-laden dust can be imagined during glacial maxima but also during times of extensive volcanism. If iron supply can be connected physically with a part or parts of the ocean that are iron-depleted, then production might be enhanced. Such a connection has been found in Papua New Guinea between a time of active uplift and probable volcanism and extraordinarily high deposition rates of opal, which can be related to standing stocks of diatoms (Wells, Vallis, and Silver 1999). Because the Pacific equatorial undercurrent originates in the convergent island arc region around Papua New Guinea, we have a direct connection between iron supply and a current system that provides a large portion of the new production in the global ocean.

Volcanism is directly connected to sea floor spreading: higher spreading rates imply higher volcanic activity at spreading centers. This might provide two connections between tectonics and life, at least in the deep sea. First, greater spreading rates may provide more nutrients from the expected increase in occurrence of hot vents, at least in the form of sulfur-dependent bacteria that can be eaten by associated animals. Second, more continuous occurrences of hot vents along a rapidly spreading ridge system might allow for larger and more continuous populations. Thus, the eastern southern Pacific spreading center, whose spreading rates are much higher than that of the Atlantic, might be expected to have less frequent shutting down of vents and therefore higher diversity. This very relationship has been shown recently to apply to mussel-related communities at hot vents, although the number of analyzed sites with different spreading rates is still low in number (Van Dover 2000). It is not yet clear that this can be connected to diversity in the shallow ocean, which might be more coupled with climate change that is driven by atmospheric processes.

The productivity–diversity argument is a classic chicken–egg problem. Does diversity foster productivity, or is it the reverse? When we look at a rain forest, we encounter an enormous level of primary productivity, and our inclination is to believe that this allows more species to “fit.” But there is a reverse argument, especially given that some of the most productive areas of the ocean are those with the lowest species diversity and the simplest of food webs (e.g., Rosenzweig 1992; Ryther 1969). Some more recent studies suggest that more diverse communities have higher productivity (Hector et al. 1999) and are more stable (McGrady-Steed, Harris, and Morin 1997) than species-poor communities. In diverse communities, more species can fill in areas of resource space that would otherwise not be exploited, and more mutualisms are to be expected with more coexisting interacting species. Thus, productivity may be an effect of diversity or, more likely, both arise from another property, perhaps environmental stability, which allows species to survive and does not cause frequent extinctions.

Long-term fluctuations in climate are imperfectly understood, but today’s conditions are not typical of all Phanerozoic time. Large polar continental ice sheets existed in the pre-Cambrian, Carboniferous–Permian, and Pleistocene, but globally equable climates prevailed in the mid-Paleozoic and Mesozoic (Figure 7.18). These periods were also dominated by great evolutionary radiations of a wide variety of unrelated phyla. The great Cambrian–Ordovician and Mesozoic expansions thus seem marked by rises in sea level, increases of volcanism, and ameliorations of global climate.

Fischer (1984) connected volcanism and global climate through the greenhouse effect. Increased volcanism may have liberated carbon dioxide into the atmosphere. As these periods were of higher sea-level stand, erosion would have been minimal, and loss of CO_2 in weathering would be suppressed. During times of low sea level, low volcanism would reduce the liberation of CO_2, and increased weathering would consume CO_2. Thus, the mid-Paleozoic amelioration was associated with high CO_2, which, in turn caused a greenhouse effect and an increase of surface temperature. The end of the Paleozoic witnessed the termination of such conditions, and an "icehouse effect" resulted in a deterioration of climate mainly at high latitudes.

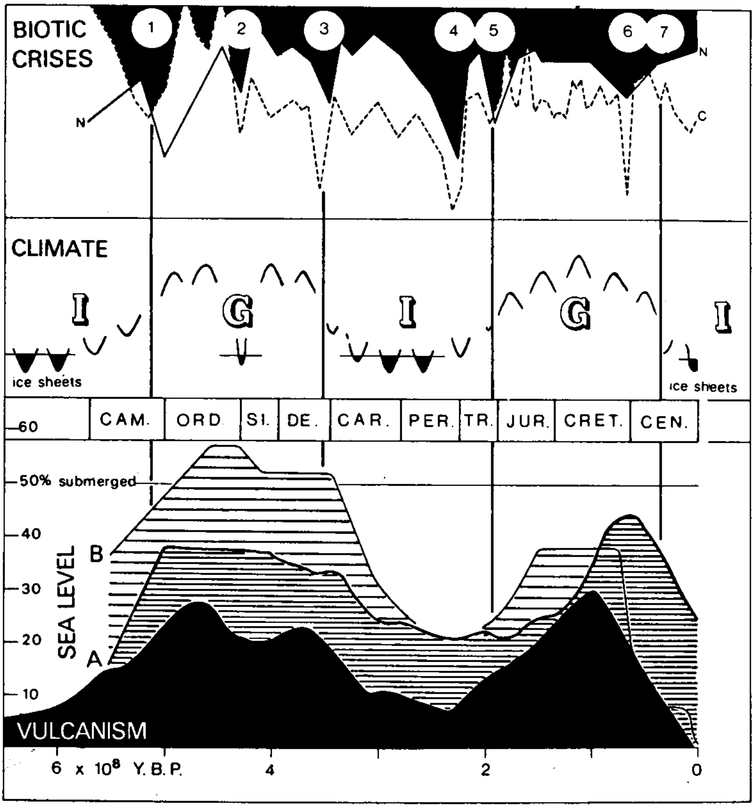

Figure 7.18. "Supercycles" of the Phanerozoic, postulated by Fischer. Sea-level curves according to (**A**) Vail et al. 1977 and (**B**) Hallam 1977b are superposed on a diagram of granite emplacement, times of glaciation, times of biotic crises (numbered) as determined by Newell (curve N) and Cutbill (curve C), and a guess of climate, characterized by either icehouse (*I*) or greenhouse (G) conditions. (From Fischer 1984, reprinted with permission of Princeton University Press.)

It is not clear whether these cited fluctuations are irregular temporal changes or regular oscillations. Fischer (1984) favored a 300-million-year cycle. The hypothesized greenhouse conditions coincide with the two major expansions of metazoan life in the Phanerozoic, but extinctions are less clear. The Permian–Triassic crisis occurred after the glaciations and is also associated with a dramatic drop in sea level. The Cretaceous extinction is not associated with a switch from greenhouse to icehouse conditions. Cold temperatures might or might not have contributed to extinctions.

In a moment of extraordinary paleontological excitement that, regrettably, has passed, Raup and Sepkoski (1984) reported a periodicity of about 26 million years in the occurrence of extinction peaks. Using a more qualitative assessment of pelagic taxa, Fischer and Arthur (1977) had previously claimed a similar periodicity of 32 million years. With the use of a family-level data set, a statistically significant series of regularly spaced peaks could be ascertained in the temporal changes of families among the 39 stages (250 million years) since the Late Permian. As Raup and Sepkoski acknowledged, both the uncertainties of the geological timescale employed and the smaller number of time units (maximum resolution of 6 million years) made such an analysis tentative, as it excluded a wide variety of factors within smaller timescales, including the Milankovitch hypothesis mentioned above. To consider an extinction important, Raup and Sepkoski used a threshold level of 2%. Using a threshold of 10%, Rampino and Stothers's (1984) reanalysis yielded a periodicity of about 30 million years. The time interval between peaks lies between 17 million years and 53 million years, a variation whose importance cannot be gauged without a specific physical or biological model. Some of the variance, or regularity, may be due to biases in the timescale employed (Hallam 1984; Hallam and Wignall 1997, p. 9). Mesozoic stage boundaries have an uncertainty of at least 5 million years, and some even larger disparities exist among different published timescales. The potential for an artificially induced periodicity can be seen in some cases, such as the Upper Triassic, where stages are each arbitrarily set at a 6-million-year duration. Periodic behavior could also be generated by a model with a strong stochastic component (Kitchell and Pena 1984).

Raup and Sepkoski's analysis (1986) of generic data revealed eight major episodes of extinction over the last 250 million years that are more pronounced than those defined by the family-level analysis. The more recent analysis identified two more extinction peaks and strengthened the estimate of 26 million years. Random simulations did not generate such strong periodicities. But how monophyletic are the groups? Patterson and Smith (1987) complained that analyses using the taxic approach included paraphyletic taxa, incurring the risk of including pseudoextinctions of groups that had surviving descendants with different taxonomic names. This problem pervades paleontological analyses, and it is too bad that it has not been resolved terribly well so far. Hallam and Wignall (1997, p. 10) parried that it is "cladistic facetiousness" to unite the dinosaurs and birds and therefore claim that the dinosaurs really did not become extinct at the end of the Cretaceous. As discussed above (see the section titled The Taxic Approach), this problem *is* significant. The increased strength of the peaks found in the analysis of genera is encouraging, however, given that genera are likely to be more frequently monophyletic than are families.

The Raup and Sepkoski periodicity hypothesis couldn't even get to the presses before many raced to find a physical cycle to match the 26-million-year periodicity. Catastrophes generated by periodic extraterrestrial events seem plausible. Two independent analyses of large body impact craters (Figure 7.19) yield a periodicity of 28.4 million years (Alvarez and Muller 1984) and 31 million years (Rampino and Stothers 1984). The phase of this cyclicity was consistent with that of the extinctions, though the numbers were small. Two different astronomical models were suggested as ultimate causes of the periodicity. The *galactic plane oscillation* hypothesis argued that the solar system oscillated about the galactic plane with a periodicity of about 33 million years. Such movements might increase the probability of contact with clouds of gas and dust near the galactic plane, which in turn might gravitationally perturb the solar system's comets and thereby increase the frequency of planetary impacts (Rampino and Stothers 1984). A pass through the galactic plane might have also influenced the earth's magnetic field and even resulted in increased atmospheric dust (Hatfield and Camp 1970; Schwartz and James 1984). The periodicity and the present arrangement of the solar system relative to the galactic plane, however, suggest that the mass extinctions took place when the solar system was farthest from the galactic plane (Schwartz and James 1984). The *distant solar companion* hypothesis argued for the presence of an unseen solar companion whose orbit passes periodically through a cloud of comets in the outer solar system, sending some of them on paths toward the inner solar system and the earth (Davis, Hut, and Muller 1984; Whitmire and Jackson 1984). A search, yet to be consummated, is on for this hypothetical companion.

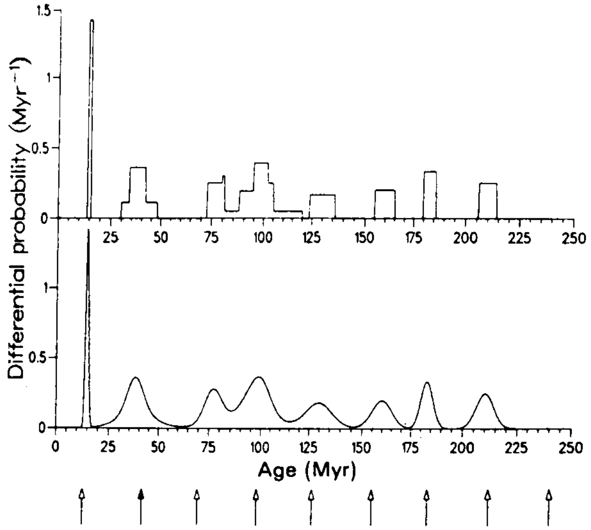

Figure 7.19. Impact craters on the earth with a diameter of more than 10 kilometers and an age of 5 million years to 250 million years. (From Alvarez and Muller 1984.)

The proximate cause of the extinctions is another matter. Presumably, an increase in cometary impact might raise dust clouds sufficient to cause a drop in insolation and a decline in climate. Much of the evidence suggests that an increase in cold climate had something to do with many of the mass extinctions in the Phanerozoic (Stanley 1983, 1984). If single impacts were important, then one might expect precipitous extinctions. Both models, however, allow for a series of impacts or events, permitting extinctions to occur over prolonged periods of time. This is a fundamental weakness for the testing of the models, as the only potentially good data we might be able to get would relate to the suddenness of the extinctions.

The periodicity argument is a slippery affair, even if it is the clearest hypothesis ever proposed to explain the tempo of extinctions. Immediately, it becomes clear that neither the amount of extinction, nor any model, compels us to do anything more than look for peaks at certain times. The amplitude of the peaks, for example, could be small or large. Thus, of 10 mass extinctions predicted, only 5 or 6 occur with any certainty, and even a definitive extraterrestrial model does not preclude episodes when impacts are minor in effect. The Late Eocene extinction, for example, comprises a groups of events and is quite small overall, relative to a number of the Mesozoic extinctions (Hallam and Wignall 1997, p. 11; Hoffman 1989). Newer timescale data make some of the spacing depart from 26 million years. Perhaps worse than that, a newer and somewhat independent large-scale assessment of family level diversity of a wide array of fossil groups found no evidence for periodicity (Benton 1995). Right now, the periodicity hypothesis can be said to be stalled.

Reprise: Are there mass extinctions? Gould (1985) characterized mass extinctions as a distinct "tier" to be considered as qualitatively distinct in the history of life. In contrast, Valentine and Walker (1987) suggested that increasing extinction in the Permian is, for the most part, a matter of degree, even though there are some distinctive effects for some taxa. Mass extinctions, although global in extent, could be the end members of a continuum of environmental perturbations that stimulated extinction and allowed the explosive evolution of replacing groups. Should we deny a special status to these extinctions, even though they may be extreme and fascinating in their own right? Miller (1997) provided evidence that some aspects of major changes in taxon richness in the fossil record constitute a composite of regional changes that are not synchronized, so we could be dealing with aggregates of independent phenomena.

The nature of mass extinctions still remains elusive. Hoffman (1989a, 1989b), with characteristic acumen and skepticism, made the case against all mass extinctions but the great one, the end-Permian. Those schooled in old-fashioned stratigraphic paleontology, like me, would have probably owned a set of index cards, with a hand-drawn picture on one side and a name and stratigraphic range on the other. I remember with clarity, even though I no longer have the cards, the single most common range of the major groups: Ordovician to Permian. I guess that a modern version of such cards (a Web page?) would be Cambrian to Permian, but still it is clear why we recognize this great extinction. It is not only because of the magnitude but also because it was truly the end of an era, and the beginning of a modern fauna, which can be recognized easily by eye, if you feel less comfortable with the glories of factor analysis. This great fact obscures other debates, such as whether the final blow came gradually, in a double burst, or as one final coup de grâce.

Declining extinction: An improvement in the quality of life? Sepkoski's (1984) analysis of evolutionary faunas produced the fascinating result that successive EFs are less and less prone to extinction. In the Ashgillean and Frasnian extinctions, for example, the Cambrian EF suffers more than the Paleozoic EF. In the Permian and Norian extinctions, the Paleozoic EF suffers more than the Modern EF. Excluding mass extinctions, family-level background extinctions have declined over geological time (Raup and Sepkoski 1982). This decline might have been in two stages. During the Permian, extinction might have been reset to a much higher level, followed by a second period of decline after the Paleozoic decline period (Van Valen 1984). Alternatively, the Permian family extinction might just have been a temporary perturbation. The successive evolutionary faunas also have progressively lower turnover (appearance plus extinction), which may make for increasing stability.

Family-level extinction rate declines during a long Paleozoic period of fairly constant taxon richness. To keep a steady state, a decline in extinction must be matched by an overall decline of originations. This is borne out by a reanalysis (Hoffman and Ghiold 1985) of Sepkoski's data (Figure 7.20).

Why should family-level extinction and origination rates decline over geological time? Van Valen argued that a decrease in probability of extinction can be explained by an increase of the ratio of positive to negative interactions among taxa. A reduction of competitive interactions might decrease extinction. Carnivores show a progressive specialization of families (Radinsky 1982), which might reflect a reduction in competition. But tiering – the presence of multiple living marine consumer layers, relative to the sediment–water interface – reached peaks of development in the late Paleozoic and in the Triassic and Jurassic (Ausich and Bottjer 1982). No long-term

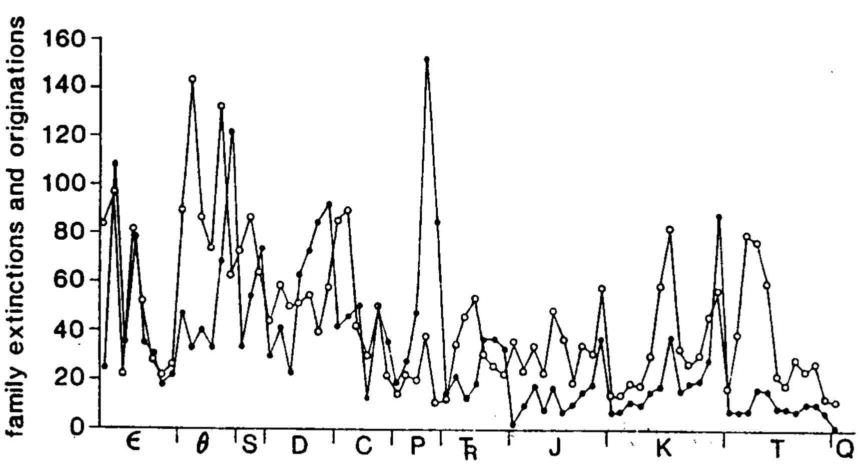

Figure 7.20. Total numbers of marine animal family originations (open circles) and extinctions (closed circles) per geologic stage. (From Hoffman and Ghiold 1985, with permission.)

increase is notable. Bambach (1983), however, showed that additional major resources have been exploited as time progresses. This suggests that the biota has been steadily invading new space; this might contribute to the decline of extinction, but it doesn't explain the decline of family-level origination.

Raup and Sepkoski (1982) suggested that the decline in extinction might reflect an increase in Darwinian fitness. This is not an argument for differences of superiority among major groups, as in mammals over reptiles. Such major shifts seem to require mass extinction. Rather, normal background extinction might have declined as fitness improved. But there is no real evidence that individual performance is related to species or family-level extinction. Unfortunately, our knowledge of extinction is limited almost exclusively to extinctions induced by humankind. But if the loss of the Brazilian rain forest is any indication, extinction is usually due to loss and degradation of habitat rather than to any particular properties of individuals.

Extinction may have declined as a result of the ratio of species numbers per families, which has been increasing steadily since the Mesozoic (Valentine 1969). If a family's representation in the world biota increases in numbers of species and its consequent ecological and geographic coverage, then the probability of extinction may decline (Flessa and Jablonski 1985; Jablonski 1986).

This explanation still does not provide a satisfactory answer to the decline in originations. Such a decline implies a long-term reduction in the production of novelties sufficient to define taxonomic families. In other words, the rate of origin of morphological diversity has decelerated over time. This is consistent with Valentine's (1986) characterization of the long-term decline of origin of basic ground plans. Since the Cambrian, no new ground plans have appeared, and a host of novel body plans appeared in the pre-Cambrian and Cambrian, never to reappear at the same level of diversity. Two concomitant processes might have contributed to this decline in origins of basic morphological diversity. First, a general filling in of resource space might have made it difficult for wholly new forms to take root later and spread. Second, as the shakeout of early ground plans occurred, perhaps by random extinction, the surviving ground plans might have slowly congealed to the point that genetic, epigenetic, and functional constraints precluded the rise of descendants with wholly different body plans. Heterochrony may be a mechanism for major evolutionary change, but wholly new phyla are unlikely to arise from chickens or clams or starfish. Our world may very well be the tangled bank conceived by Darwin, even if the exact mechanisms of constraint are more diverse than he conceived.

In the first edition of this book, I ended this chapter by stating the belief that the origin of phyla was an erratic process, perhaps never to be duplicated again in terms of diversity of body plans. Well, let's look at the final chapter now!

The Main Points

1. Studies of diversity, appearance, and extinction depend on the taxic approach, in which given taxonomic levels are employed as indicators of biotic diversity. In some cases, abundance at, say, the family level is believed to be linearly related to numbers of species. In other studies, the family level is taken to be a measure of diversity of major adaptations.

2. Multivariate statistical analyses permit the resolution of marine fossil taxa into a series of evolutionary faunas that behave statistically independently of one another. The exact ecological or evolutionary significance of these associations is poorly understood.
3. The three evolutionary faunas successively achieve dominance in the fossil record.
4. Taxonomic longevity seems to vary among phyla; though average longevity may differ, the variability of longevity cannot be distinguished from a model of stochastic appearance and extinction.
5. Taxon diversity appears to be stable for long periods of geological time. The waxing and waning of the evolutionary faunas has been explained as the result of a three-stage model of growth in diversity toward an equilibrium. The apparent plateaus in diversity have been differently explained as being due to a negative feedback imposed by large-scale extinction events. Some detailed studies suggest that steady-state diversity levels are maintained by a balance of appearance and extinction.
6. Biogeographic provinciality influenced overall diversity. The Permian extinction was accompanied by a decrease in the number of marine provinces. This might have been related to a deterioration of world climate.
7. The Phanerozoic has been punctuated by periods of major extinction. Some were very severe, though it is generally not clear whether species were just extinguished or speciation also was depressed. It has been suggested that the major extinctions were qualitatively different from so-called background extinction; this can be seen to a degree in patterns of extinction as related to parameters such as the biogeographic range of a species. On the other hand, the major end-Cretaceous extinction showed selective eliminations that can be related to individual differences in adaptation. This is not so different from what might be expected during a fairly minor environmental shift, only on a larger scale.
8. Ultimate causes for extinction are poorly understood. Cycles related to the precession of the earth's rotational axis may cause strong changes on the scale of 10^4 years. A periodicity in extinction of about 26 million years has been demonstrated for the post-Paleozoic extinctions. This periodicity has been related to several plausible astronomical periodicities, and the presence of iridium and shocked quartz at some horizons has supported the suggestion of bolide impacts as the ultimate cause of some extinctions. The actual pattern of extinction, however, is complex, and some extinctions occur before the hypothesized impacts. Unfortunately, the temporal level of resolution in the famous end-Cretaceous event is not less than 100,000 years. The proximate causes of extinction are poorly understood but probably include changes in climate, sea-level changes, and climatic changes induced by rearrangements of continents.
9. The family-level extinction rate declined through the Phanerozoic. This is matched by a similar decline in originations. The explanation for this observation is not clear. Families may have become more species-rich over time, and this may buffer their extinction, because, as time progresses, the extinction of any one species is less likely to result in the extinction of an entire family. This, however, would not adequately explain the decline in family-level origins. A gradual loss of potency to produce more families might be explained by increased competition, or the gradual increase in developmental constraints. The latter might be related to the pattern of declining rates of origin of higher taxa.

CHAPTER 8

A Cambrian Explosion?

> All God's critters got a place in the choir
> Some sing low, some sing higher,
> Some sing out loud on the telephone wires,
> And some just clap their hands, or paws, or anything they got now
>
> – Bill Staines, 1979

Introduction

No paleontological challenge rises higher above the landscape of evolutionary biology than the Cambrian Explosion of animal life. If the fossil record is to be taken literally, the Tommotian and Atdabanian stages of the Cambrian encompass the appearance of all but one of the modern bilaterian triploblastic animal phyla (Chen, Dzik, Edgecombe, Ramskøld, and Zhou 1995; Conway Morris 1989). The Manykaian stage presages this eruption with the appearance of a variety of spines and shells of more problematic groups (Bengtson 1977, 1992), and some shelly fossils are found in latest Precambrian rocks, even with evidence of predatory boreholes (Bengtson and Zhao 1992). The metazoan cornucopia pours out brachiopods, arthropods, echinoderms, priapulids, mollusks, onycophorans, and the rest – even chordates – all in rocks representing a breathtaking sprint of less than 10 million years (Bowring et al. 1993; Grotzinger et al. 1995). Only one readily preservable phylum, Bryozoa, still stubbornly refuses to be discovered in the Cambrian, but we can be sure that it is only a matter of time before it will be.

This is the wonderful story told by the rocks, but how sure can we be that what is "writ in stone" is all that reliable? Is it within the range of reason that all of the phyla could have arisen and diverged in so short a time? Is the preservation so good that we can be sure that no echinoderms, arthropods, or mollusks are likely to be discovered in Precambrian rocks? Indeed, what are the stakes behind a refutation of the explosion hypothesis? Is it possible that one can refute the explosion hypothesis without ever discovering a fossil in the Precambrian? These are the subjects of this chapter.

Stanley (1976), in an article brimming with interesting ideas about the Cambrian, articulated the two important questions raised by the apparent sudden appearance of Cambrian fossils:

1. Why do many distantly related skeletal phyla and classes seem to appear almost simultaneously in the fossil record?
2. Why do important skeletal taxa appear at high levels of complexity? (Stanley 1976, p. 209).

These two questions have occupied the attentions of paleontologists for about 150 years, and they show no sign of getting quick answers.

Origins of the Problem

There could be no Cambrian Explosion without the development of the notions of a geological timescale and the realization that there was a beginning to the animal fossil record. Lacking an absolute timescale, geologists could date rocks only by means of their fossils. Such a relative timescale was developed principally during the nineteenth century, when all our familiar period names were coined to denote units of geological time, whose absolute time spans were unknown.

By the 1830s and 1840s, it became clear that rocks of England and Wales contained a succession of fossil faunas that ranged from those that included many living forms to those with completely extinct biotas, connoting great antiquity. The notion of a beginning to the animal fossil record could already be found in William Buckland's 1836 contribution to the famous Bridgewater treatises. Soon a controversy arose over the nature of the oldest Paleozoic rocks. Roderick Murchison, an early officer of the Geological Society of London, named the Silurian system for a characteristic fossil marine fauna found on the Welsh borderland. Adam Sedgwick, the first active occupant of the Woodwardian Chair of Geology at Cambridge University, claimed to find rocks even more ancient in central Wales, which he termed the Cambrian.[1] A debate ensued as to whether such older rocks bore a primordial fauna, distinct from that of the Silurian. The waters were muddied when Murchison later discovered Silurian-type faunas overlying crystalline and presumably abiotic rocks in Sweden, suggesting a beginning of animal life with Silurian-type faunas. But Murchison enlarged his concept of the Silurian to include slightly older faunas, thus excluding the Cambrian and infuriating Sedgwick, whose claim for a distinct biota was co-opted into the Silurian concept. But a pre-Silurian fauna of (what are now recognized as) Cambrian trilobites was found later in Bohemia, in Sweden, and even in Sedgwick's original Welsh Cambrian-age sites, thus vindicating Sedgwick's notion of a Cambrian Period. The Cambrian Period was not officially installed until the 1870s, after intermediate rocks were assigned to the Ordovician Period. Although some of this debate might have involved a competition for priority on names of geological periods, it also established the approximate beginnings of the Paleozoic, below which there were no apparent traces of animal life.

Darwin contemplates the beginning of it all. The controversy between Murchison and Sedgwick established a geological beginning to the record of animal life.

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[1] He was aided one season by a Cambridge University student and native to the Welsh borderland, Charles Robert Darwin.

Murchison's error in thinking that fossiliferous rocks overlying crystalline rocks marked the beginning of animal life has reappeared in many subsequent geological controversies. We have frequently mistaken nonpreservational gaps in the geological record for absences of biological activity, which was the core of Darwin's skepticism of the suddenness of the Cambrian explosion. The controversy of a primordial fauna was more or less settled during the writing and revision of *The Origin of Species by Means of Natural Selection*; Darwin used the term *Silurian* in the first edition, but the Cambrian system was mentioned by the issue of the sixth, and last, edition in 1872. In general, Darwin had to grapple with paleontological evidence in all parts of the geological column that faunas had appeared abruptly, with many distantly related new fossil groups springing into being all at once. Darwin was skeptical that evidence for sudden origins would remain the case for long, and he alluded to the many parts of the world where fossils had not been searched for as yet. He also noted a number of exciting discoveries that extended the range of a given group to a point before a previously reckoned abrupt appearance.

Darwin was not so sanguine about the likelihood of future fossil finds before the Cambrian, which appeared to mark the abrupt beginning of animal life. Darwin (1876) saw the beginning as likely to be gradual and long before the Cambrian:

> Most of the arguments which have convinced me that all the existing species of the same group are descended from a single progenitor, apply with equal force to the earliest known species. For instance, it cannot be doubted that all the Cambrian and Silurian trilobites are descended from some one crustacean, which must have lived long before the Cambrian age, and which probably differed greatly from any known animal. [p. 327]

Darwin noted that many fossils in rocks older than the Silurian had been discovered down to the Lower Cambrian and even perhaps in older Canadian rocks. Darwin (1872) was still able to resort to the possibility that further discoveries might fill in this obvious gap in the record:

> I look at the geological record 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. Each word of the slowly changing language, more or less different in the successive chapters, may represent the forms of life, which are entombed in our consecutive formations, and which falsely appear to have been abruptly introduced. On this view the difficulties above discussed are greatly diminished, or even disappear. [p. 331]

Cloud's challenge – the Cambrian was the beginning of it all. Darwin's surmise, that paleontologists would eventually discover Precambrian animal fossils, did not pan out. Further worldwide collecting only heightened the sharpness of the Cambrian beginnings of animal fossils. By the turn of the century, a global Cambrian stratigraphy was sufficiently well developed to present a convincing case for the abrupt Cambrian appearance in the geological column of animal fossils. There were ambiguities, however. Walcott (1899), for example, found Precambrian (Middle Proterozoic) vertical "burrows" in Montana, which he named as two species of *Planolites*. These have been accepted by some as bona fide metazoan traces (Alpert 1975) but discounted by others (Cloud 1968, Hoffman 1992). But overall, paleontologists could see no strong evidence refuting the idea of a sudden appearance of fossils in the Cambrian. John W. Evans (1912), although noting the possibility of a few Precambrian burrowers, saw the Cambrian appearance as a true evolutionary event and felt that it might have been stimulated by the extensive volcanism recorded in rocks near the base of the Cambrian. He discounted other environmental hypotheses, such as the lack of lime for skeletons, given that there was ample Precambrian limestone. Evans (1912), however, fell in with Darwin as to the suddenness of the event and believed that a late Precambrian episode of exposure was a period during which no fossils were preserved:

> It was the gradual advance of the sea over these terrestrial accumulations that marked the coming in of the Cambrian Period, and we need not be surprised that the marine fauna had changed to a very considerable extent in the long interval unrepresented by marine deposits. [p. 344]

The sudden appearance of the Cambrian of many unrelated groups was proof to Evans that a long period of evolution must not have been preserved in the rocks. Given the apparent long range of fossil invertebrate species (ca. 6 million years), the distinguished paleontologist J. Wyatt Durham (1967) also thought that the missing Precambrian record must have been temporally quite extensive.

Evans's article reflected what was to become a pattern in paleontological inference, which involved the search for global-scale climatic changes as the cause of evolutionary eruptions and mass extinctions. Others looked toward biological interactions, such as predation, or the appearance of key innovative adaptations as the magic bullet (Stanley 1973, 1976). Central in the Cambrian debate was the appearance of many distantly related groups with skeletons. On one side was the opinion that the rise of groups with skeletons was a response to the advent of predation (Stanley 1976); alternatively, a global change in geochemistry was thought to stimulate the Cambrian explosion. Calcareous skeletons, for example, were found to be rare in modern dysaerobic environments, which suggested that an increase in oceanic dissolved oxygen might have stimulated the appearance of skeletons (Berkner and Marshall 1965; Rhoads and Morse 1971).

The global changes that might have stimulated the Cambrian rise of animal life were conflated with the question of preservation. If, for example, the rise of predation stimulated the near-simultaneous appearance of distantly related skeletonized phyla, then it might be possible that a long period of Precambrian evolution predated the Cambrian appearance. On the other hand, fossil burrows also increased in abundance and diversity just below the base of the Cambrian, which would weaken the skeleton-predation hypothesis (see Grotzinger et al. 1995; Macnaughton and Narbonne 1999 and references therein). Enter Preston Cloud. It would be incorrect to say that Cloud invented the Cambrian Explosion, but he certainly dealt with the data of the fossil record more directly than did previous workers. In a prescient article in 1948, he pointed out that

> The appearance of diversified multicellular animal life in the Cambrian may actually have been almost as sudden as the record suggests, an instance of eruptive evolution of the root stock of animal life itself. [p. 346]

Of particular importance was Cloud's debunking of many so-called Precambrian fossils, mainly identified as burrows and surface trails of macroinvertebrates with hydraulic skeletons (see Fedonkin and Runnegar 1992; Hofmann 1992). Cloud did not see a true Cambrian Explosion as unexpected, as it conformed to his experience in reckoning the rapidity of appearance of many fossil groups, such as the terebratuloid brachiopods, which first appeared as a diverse group in only a few million years in the latest Silurian and early Devonian. Cloud noted that this general aspect of *eruptive evolution,* as he called it, conformed perfectly to George Gaylord Simpson's characterization of the fossil record as punctuated by very short term evolutionary radiations that produced a great deal of morphological diversity (Simpson 1944). As Simpson was the preeminent paleontologist of the twentieth century, it is likely that his conception of evolutionary bursts was coopted, consciously or subconsciously, into the fabric of later ideas on the Cambrian Explosion. Cloud saw the eruptive phase as one of evolutionary plasticity, perhaps enhanced by increased mutation rates and "paedomorphic tendencies."

One must remember that Cloud's characterizations in 1948 came at a time before there was much quantitative appreciation of diversity changes in the fossil record. Mostly, he had to go by individual accounts, usually qualitative and intuitive, of first appearances of fossil groups, leavened by his own extensive experience. It wasn't until a few years later that Norman Newell's classic paper on periodicity in invertebrate evolution appeared, which quantified what was then known of the waxing and waning of fossil groups (Newell 1952). Using compilations at the generic level of better-preserved marine fossils, it was clear that times of diversification and extinction were simultaneous across a wide spectrum of distantly related phyla. This justified Cloud's belief that evolutionary eruptions were widespread and cut across the details of biological specificity. Cloud and Newell could assert that some set of environmental changes, hopefully readable in the rocks, set the pace of evolutionary radiations and extinctions. Newell (1952) thought that submarine diastrophism (readily likened to modern notions of sea-floor spreading and crustal deformation) caused fluctuations in sea level, which in turn caused evolutionary radiations and extinctions.

These ideas lay fallow for a while until Cloud's important 1966 lecture at Yale University on the Precambrian biosphere and Cambrian life (see Cloud 1968). Cloud was a commanding figure, and his interests and geological background made him the perfect person to have the perspective to understand the potential meanings of the dawn of animal life and, for that matter, the origin of life itself. As a graduate student, he arrived at Yale thanks to the encouragement of the great Paleozoic brachiopod expert Charles Schuchert and worked under the direction of Carl O. Dunbar, one of the twentieth century's great invertebrate biostratigraphers. With this background, rocks and fossils were his natural stomping grounds, and he spent many productive years at the United Stated Geological Survey. But his intellectual development led him toward global theories of evolutionary innovations and eventually to an interest in exobiology. He spent a significant part of his career at the University of California, Santa Barbara, worrying about how extraterrestrial life and the origins of life could be detected and understood. He probably was the most broadly experienced invertebrate paleontologist we are ever liable to encounter, and the breadth of his work set the stage for a new ecumenism in styles of paleontological inference.

Cloud's theory is simple (Cloud 1968): The Cambrian Explosion was a real diversification, and fairly sudden. It did not matter to him whether it happened in a few million years or a few more. The rocks spoke clearly, however, that the rise of triploblastic metazoans was sudden relative to the broad context of geological time. In cementing this conclusion, Cloud had to deal with a raft of so-called Precambrian body and trace fossils, and he dismissed all of them as sedimentary structures, algae, or other types of misinterpretations.[2] The sudden appearance of such diverse groups struck Cloud as evidence that the animal kingdom was polyphyletic; given the evidence, he inferred four possible independent rises of invertebrate groups, but he warned that the evidence was insufficient to be sure about details.

With this interpretation, Cloud sought to find a global change that stimulated the rise of so many unrelated groups at an auspicious time such as the Cambrian. He favored the increase of atmospheric oxygen as the trigger of the Cambrian explosion. In rocks younger than about 1.8 billion years, there was evidence of atmospheric oxygen, which was thought to be incompatible with the deposition of more ancient rocks with banded iron formations. Thus, oxygen perhaps began to increase 1,800 million years ago and might have reached a threshold conducive to large body size at the beginning of the Cambrian (Berkner and Marshal 1965). Some of Cloud's argument has foundered. He thought the presence of uraninite to be evidence for anoxia, but uraninite can form in localized environments in an oxic atmosphere. The partial pressure of oxygen might have reached about 1% of the current atmosphere at least 2 billion years ago, which suggests that animals could have lived in profusion, although perhaps not at large body size.

Although the oxygen evolution theory was certainly speculative, Cloud left us with a confrontation. He made us face the rock record as one of facts and left us with a mantra that is being chanted and followed today, to the credit of all paleontologists engaged in the Cambrian debate:

> Is it surely a fossil or the work of an organism? Does it represent an authentic metazoan? And is it surely endemic to rocks whose stratigraphic position is such that they cannot reasonably be included in the Paleozoic? For bold though we may be in building hypotheses in context with the framework of knowledge available, that framework itself may be extended beyond known limits only by demonstrable facts. [Cloud 1968, p. 51]

The Early Cambrian Is Established as the Cornucopia of Animal Life

In subsequent decades, the Cambrian was investigated intensively by many paleontologists around the world. By and large, its subdivisions (Figure 8.1) were diagnosed on the basis of successions of fossil faunas, dominated mainly by trilobites, arthropod relatives of unknown affinities, and inarticulate brachiopods. Trilobites,

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[2] Cloud later softened on seeing a deep Precambrian body fossil that he allowed might be a true annelid (Cloud 1986).

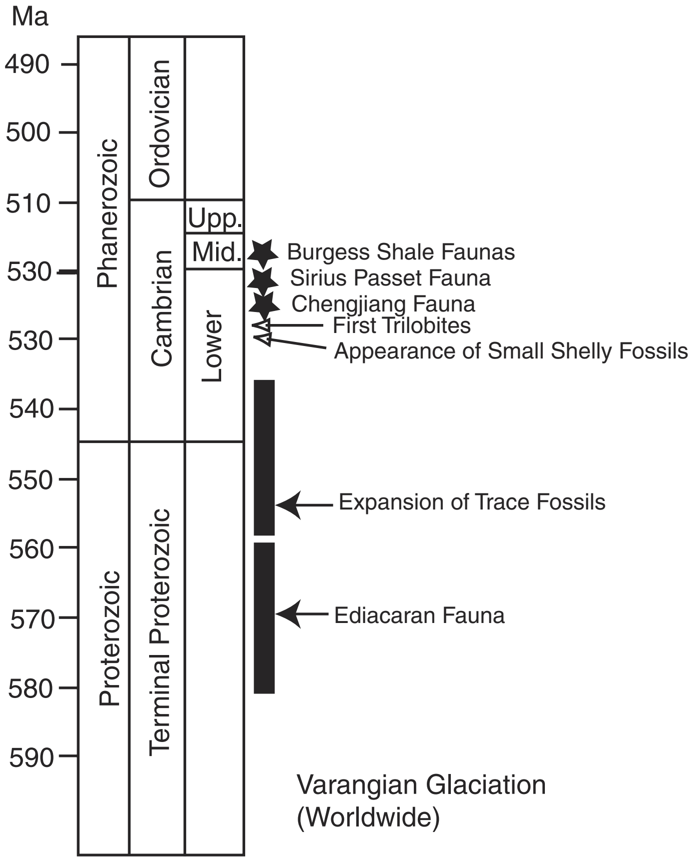

Figure 8.1. The location of the Cambrian in geological time with some important fossil occurrences and events. (After Briggs, Erwin, and Collier 1994).

although diverse, were morphologically simple relative to other arthropods, with very little differentiation among limb pairs. They were therefore taken to be near the ancestral part of the arthropod tree. Inarticulate brachiopods were abundant suspension-feeding epifauna and infauna and could be used, along with trilobites, to designate biostratigraphic zones. Many other groups were also found, including a number of members of the phylum Echinodermata, that could not be safely classified with any of the extant five classes.

Although the more typical Early Paleozoic animal groups appear in one of the earliest stages of the Cambrian, the Atdabanian, it is in the Manykaian and Tommotian stages that we more or less suddenly see the appearance of a large group of enigmatic shelly fossils, along with more familiar forms in the Tommotian. This can be seen, for example, in sections found in Siberia, the place where the "golden spike" has been established to accurately mark the type of Early Cambrian sequences. Nearby volcanic breccias can be dated at 544 million years ago. In the Manykaian, one encounters a variety of plates and spikes of uncertain relation to extant invertebrate groups. Upsection, one encounters beds of small enigmatic cone-shaped fossils known as conularids, among other enigmatic forms. Problematic shelly fossils of this stage are found worldwide, including eastern Massachusetts, eastern Washington, Siberia, Australia, the Kalmarsund and other areas of southeastern Sweden, and the Welsh borderland. An example is the *Mobergella* fauna (Figure 8.2), found throughout Europe, with representatives in Central Asia and New York, which is dominated by an enigmatic bilateral valved fossil containing radial pits that may be muscle scars (Bengtson 1977; Conway Morris and Chapman 1997). Mobergellan shells appeared to grow by accretion and were composed of primary phosphate. This is the beginning of abundant shelly fossils in the Paleozoic record. Further upsection, in the Tommotian, these give way suddenly to the more typical denizens of the Cambrian, including trilobites and brachiopods. At the very base of the Tommotian, one sees the first appearances of the panoply of the typical Cambrian fauna. At this time, we already encounter biogeographic structure with two major and several distinct minor provinces (Fortey and Owens 1990a; Fortey, Briggs, and Wills 1996).

Radiometric dating has established a new and higher level of confidence on the dating of the Cambrian. Furthermore, the dating gives us a possible story of spectacular evolution. Uranium–lead dates from zircons establish the beginning of the Cambrian at 544 million years ago. Furthermore, the oldest Manykaian stage lasted no less than 10 million years. Finally, the next two stages, where the appearances of the modern phyla are concentrated, lasted no more than 5 million to 10 million years (Bowring et al. 1993). In other words, the Cambrian Explosion of animal phyla, if the fossils tell the whole story, occurred in a geological instant!

I have to take a few sentences to mention the sad question of what it means for an event to occur in a "geological instant." I would say that it means little. As evolu-

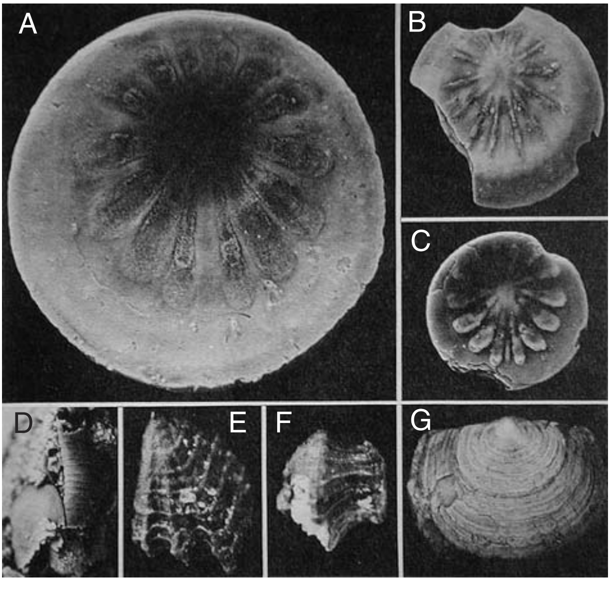

Figure 8.2. Examples of the first shelly fossils of the *Mobergella* fauna, found worldwide. **(A–C)** Species of *Mobergella*; **(D)** *Hyolithellus* species; **(E–F)** *Camenella balthica*; **(G)** *Micromitra undosa.* (From Bengtson 1977, with permission.)

tionary biologists, we have no theory to set constraints on the rate of evolution or the pace of evolutionary radiations. If all of the animal phyla appeared in 1 million years, would we be surprised? Perhaps, but our conclusion would be emotive, because there is no evolutionary principle we know well that prevents it. Seven days? No, it is not possible. A million years? Who knows?

The Ediacaran Challenge

The only widely accepted serious major challenge to the Cambrian origins story is a fauna first discovered by R. C. Sprigg in the Ediacara Hills, 600 kilometers north of Adelaide, Australia (Glaessner 1984), whose great variety includes a number of apparent coelenterates and perhaps a number of triploblasts. Subsequently, this fauna has been found worldwide, except in Antarctica, dating from approximately 600 million years ago to 620 million years ago to some time in the very early Cambrian. Most of the abundant Ediacaran fossils and burrows are concentrated in rocks of just a few million years before the 544-million-year base of the Cambrian (Grotzinger, Bowring, Saylor, and Kauffman 1995). Fossils that appear to be triploblast animals are in rocks no older than 565 million years (Grotzinger et al. 1995). Ediacaran fossils, at the upper end of their range, have been found commingled with Burgess Shale–like Cambrian fossils (Conway Morris 1993), and deeper water Ediacaran fossils have been found in rocks as young as 510 million years old (Palmer 1995). The Ediacaran-type faunas reach their peak diversity only a few million years before the Cambrian (Grotzinger et al. 1995), as does a rapid increase in the diversity of preserved burrows, which reach a peak just before the start of the Cambrian (Fedonkin and Runnegar 1992).

The Ediacaran fauna, therefore, does not extend the dawn of animal life much further back, but it does present us with a range of enigmatic fossils, few of which can safely be included in the modern cast of animal characters up the section in the Atdabanian. Seilacher (1985) argued that many of the Ediacaran forms represent rather inactive "mattresses" that might have been compartmentalized, which absorbed dissolved organic material from the water by diffusion. The large *Dickinsonia,* classified by Glaessner as a polychaete (Glaessner 1984), actually fits Seilacher's hypothetical functional description quite well. Some of the Ediacaran animals might therefore be an independent episode in animal evolution, comprising the so-called Vendobionta, a sister group to the entirety of the Animalia (Buss and Seilacher 1994). A detailed character analysis, however, is wanting for this idea, despite its intriguing nature. Certainly, the evidence demonstrating Ediacaran fossils in Cambrian strata (Conway Morris 1993; Palmer 1995; Grotzinger et al. 1995) precludes the hypothesis of the Ediacaran faunas as a Precambrian failed evolutionary experiment.

The question of Ediacaran true animals remains open. Consider the triradiate *Tribrachidium* (Figure 8.3). This disc does not have all of the features we expect of a primordial echinoderm, but trifold symmetry is found in Cambrian stem-group echinoderms. A pentameral disc, *Arkarua,* with a pentameral arrangement of grooves on its oral surface, has been found in the Pound Quartzite in the Flinders Ranges of Australia and bears a resemblance to Cambrian edrioasteroids (Gehling

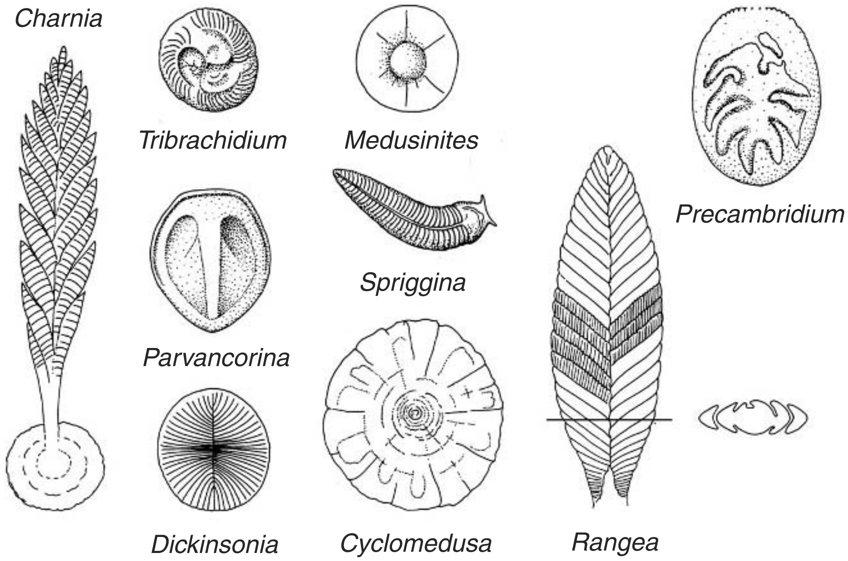

Figure 8.3. Some Ediacaran-age fossils. (After Glaessner 1984.)

1987). The Ediacaran *Parvancorina* somewhat resembles a mature version of the early Cambrian *Naroia,* an unusual arthropod with an exoskeleton composed of two large shields that has been concluded to be the sister group of the trilobites (Fortey et al. 1996). Grotzinger, Watters, Knoll, and Smith (1998) described a small (1-centimeter-wide) goblet-shaped animal of overall hexagonal symmetry, which has proven to be bilaterally symmetrical. It seems likely that more such enigmatic fossils will be discovered, but we are not close in understanding their phylogenetic relationships, or even their functional morphology.

Seilacher devised a classification of Vendian lifestyles for Ediacaran-style animals. They include

1. Mat encrusters
2. Mat scratchers
3. Mat stickers
4. Undermat miners

All of these adaptations depend on the presence of a strong biomat, probably dominated by microbial organisms such as those that construct microbial mats today. The Australian fossil *Radulichnus,* for example, is probably a series of grazing scratches, perhaps generated by grazing by the body fossil *Kimberella,* which has been argued to be an ancestral mollusk (Fedonkin and Waggoner 1997). Mat stickers included tube-making animals that probably stuck in the mat and might have had suspension-feeding tentacles. Undermat miners include a Cambrian fossil *Eochondrites* and a putative 1-billion-year-old fossil that has been found in Mesoproterozoic sandstones in India (Seilacher, Bose, and Pfluger 1998). The exact date of this locality is in hot dispute. In the Vendian Nama Formation of Namibia, a tubular fossil a few millimeters long has been found and was attached to hard surfaces, suggestive of suspension feeding (Grotzinger et al. 1998). Again, these occurrences are too scattered to tell a phylogenetic tale, but they do give whisperings of a diverse benthic fauna, including bilaterians.

While the phylogenetic links of the Ediacaran fauna are unclear, what is clear is the apparent large body size and the lack of mineral skeletonization of all species described in the fauna. We pay special attention to the lack of skeletons because they are so prominent later in the Cambrian biota. On the one hand it is no special thing to find lots of non-skeletal forms. After all, most of the living invertebrate phyla lack skeletons. The size is another matter. It may be that atmospheric oxygen was now in quantities sufficient to support larger-bodied animals, including the crescendo of animal forms appearing near the base of the Cambrian that have hydrostatic skeletons. The flattened body forms of many of the Ediacaran species might be explained by oxygen that was concentrated enough to allow larger body size but not so abundant as to permit anything more than body forms that relied upon diffusion across a body wall and sluggish life styles, perhaps involving the presence of symbiotic algae. This would be consistent with the great abundance of medusae, which might have been essentially benthic and associated with symbiotic algal forms like zooxanthellae.

Ediacaran preservation is, like the Burgess Shale, of a special nature and preservation problems cloud the potential temporal distribution of Ediacaran faunas. These faunas are preserved in shallow-water sandstones, which were deposited in fairly quiet water. There is no evidence of vertical burrowing until just before the base of the Cambrian, suggesting that the Ediacaran world lacked large animals with hydraulic skeletons. Indeed, it seems likely that the sediment surface was covered with a dense microbial mat, which would have been destroyed with the advent of burrowing animals. Thus, although Ediacaran fossils have now been found in the Lower Cambrian, the potential for preservation of this special microbial mat/sand biota must have radically diminished in the Early Cambrian as larger burrowers appeared.

The Burgess Shale and Charles D. Walcott

I feel a connection to Charles Walcott because my Stony Brook colleague, a descendant of the Boston Brahmin Walcott family, is a blood relation of this great paleontologist. Ben Walcott's wife Roslyn (a geologist) looked up Charles Doolittle Walcott in the Walcott family "stud" book, and he proved to be an "unimportant" member of the family. So it goes with bluebloods, for not only was Walcott one of the greatest paleontologists to walk this earth but also, he distinguished himself as the fourth secretary of the Smithsonian Institution. His upstate New York origins were humble, but his love of fossil collecting led to a position working for the great New York State paleontologist James Hall and eventually to a position in the United States Geological Survey. His wisdom and administrative acumen served him well and he rose to be chief of the Geological Survey, acting assistant secretary of the Smithsonian, and secretary of the Carnegie Institution of Washington, D.C. (Yochelson

1996, 1998). But throughout his career, Walcott remained a dedicated geologist and paleontologist, being especially well remembered for his comprehensive work on the trilobite-based biostratigraphy of the Cambrian in North America and even the discovery of the oldest vertebrate (at the time, and for decades thereafter) in the Ordovician Harding Sandstone. His work was titanic, despite his achievements in government and his position as an advisor to presidents. This will give solace to administrators who often feel written off the face of the academic earth, once they don the mantle of "administrator," one of the most despised terms among scholars, who often feel a sense of automatic superiority, even thought it might just be that they themselves are not suited for positions of leadership.

Of course, Walcott's place in history is identified most with his discovery of the Burgess Shale, surely the greatest invertebrate paleontological find ever. Although the actual discovery story is probably enshrouded in legend (Gould 1989; Yochelson 1996), this much is clear: Walcott and his party, which included his wife and children, found a spectacular fauna of hundreds of animal species, most preserved as carbonaceous films on the bedding planes of the shale with faithfully preserved soft parts, the likes of which had never been seen before in Cambrian fossils. The usual array of trilobites and a few other invertebrates seen in the region (which Walcott was actually collecting) were amplified (Figure 8.4) by beautifully preserved cnidarians, worms, crustacea, priapulids, and a raft of creatures that could not be easily classified by Walcott into existing taxa.

Walcott began the Burgess Shale expeditions with his discovery in the summer of 1909 and continued visiting and collecting from the site until 1924, collecting prodigiously and promptly describing specimens and publishing reports on them. His dedication knew no lapses, even in the face of the shattering news that his wife had died tragically in a train accident. Within the month, he made his way out to his beloved field sites in British Columbia, near the town of Field.

Yochelson (1996) accurately characterized Walcott's efforts, both in field collection and specimen collecting, as among the very most spectacular achievements in paleontology. Remember that this work was done in the waning years of his field career and yet he managed to reach remote sites on horseback, helped with the removal of overburden, and split tons of rock samples, leading a rather small party, which he trained. Whittington (the next great collector of the Burgess Shale) estimated that Walcott had collected a spectacular 60,000 fossils (Whittington 1985); specimens of *Marella*[3] alone filled one museum cabinet, 3 feet high (Yochelson 1996). Considering the remoteness of the site and the smallness of the party, let alone the access only by horseback, Walcott's personal effort and leadership produced the greatest collecting achievement in invertebrate paleontological history.

These collections opened a spectacular window onto Middle Cambrian times. Without this fauna, our perception of Cambrian seas would have been restricted at the time to a relatively depauperate fauna of trilobites, brachiopods, and a few other invertebrate species. But the Burgess Shale fossils included a bewildering array of forms, many of which did not fit comfortably into extant groups. In classifying the

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[3] The most common Burgess Shale fossil.

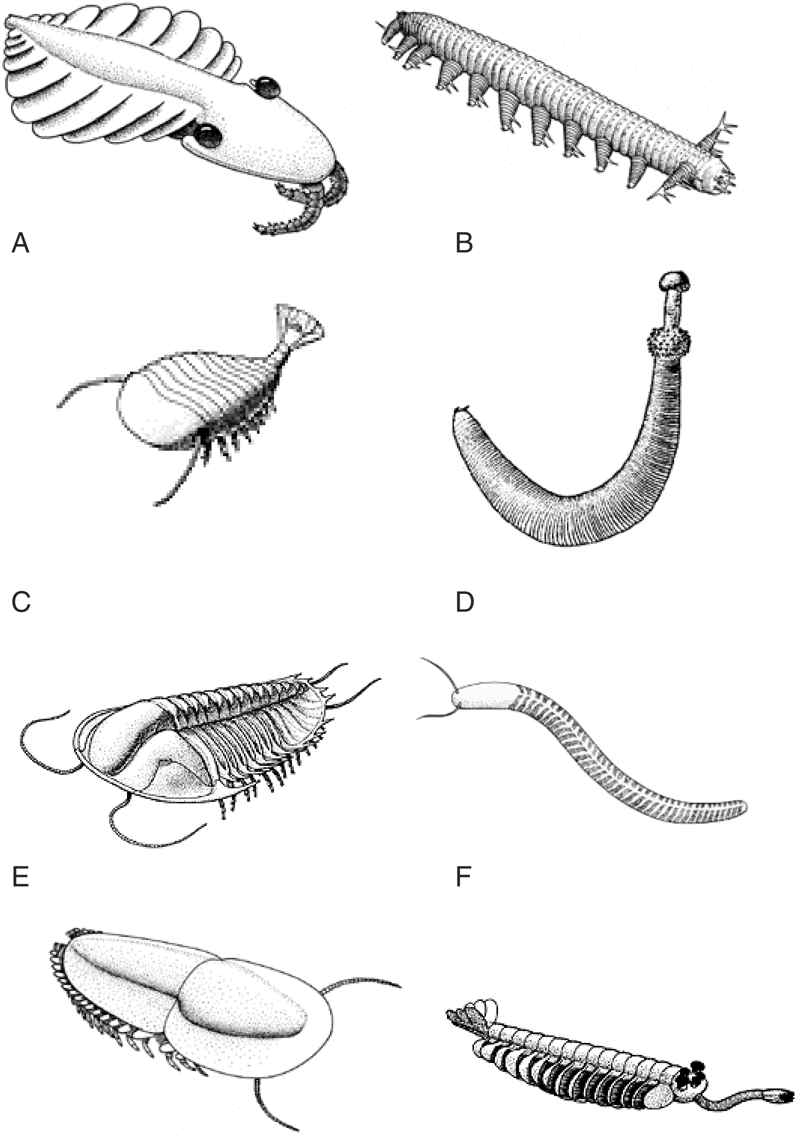

Figure 8.4. Some animals of the Burgess Shale that are mostly soft bodied and not found as well preserved or at all in typical coeval fossil localities. (**A**) *Anomalocaris,* systematic status unknown; (**B**) *Aysheaia,* onycophoran; (**C**) *Sidneyia,* arthropod; (**D**) *Ottoia,* priapulid; (**E**) *Naraoia,* two-lobed trilobite; (**F**) *Pikaia,* chordate; (**G**) *Olenoides,* trilobite; (**H**) *Opabinia,* status unknown. (Drawings reprinted with permission of Smithsonian Institution.)

fossils Walcott collected and prepared, it is clear that he lived within the restrictions of systematic practice of the time, largely imposed by the British *Treatise on Zoology.* Contemporary taxonomic practice constrained him to place many arthropods within the extant class Crustacea. But his taxonomic decisions should not be imprinted with any deep philosophical meaning, as Walcott had, only a few years previously (1894), recognized the Trilobita and Merostomata as classes separate from the Crustacea (Yochelson 1996).

The provenance of the Burgess Shale is of great interest, as it involves a very special preservation that gave us filmlike fossils of soft parts of a large variety of invertebrate fossils. Looming over the shale is a shallow-water dolomite carbonate escarpment (Cathedral Formation), which is a preserved shallow-water complex, perhaps resembling the modern Grand Bahama Bank. Beneath what must have been a submarine carbonate cliff was the Burgess Shale, part of a deeper water and seaward deposit (Stephen Formation) that contains a soft-bodied fauna that has subsequently been found to be widespread in western Canada (Butterfield 1994). The Cambrian submarine escarpment might have been as high as 160 meters (Briggs et al. 1994).

The exquisite preservation of Burgess Shale fossils resulted from downslope turbidity flows, which transported and rapidly buried marine benthos. The Burgess Shale consists of well-layered beds that are coarse at the bottom and decrease in grain size up the bed, which suggests episodic deposition. The fossils themselves are preserved helter-skelter, in many nonlife orientations. All this suggests that the animals did not live where they were deposited and were carried with the downslope currents. These conditions might have been accompanied by bottom-water anoxia, and, therefore, presence of hydrogen sulfide on the bottom, which slowed down aerobic decomposition that normally would have erased the potential for a soft-bodied fossil record. It is also possible that the clay-mineralogical content of the sediment also enhanced the potential for delicate preservation by clay binding with organic molecules and sequestering them from decomposition (Butterfield 1995). The fossils are organic films, covered by aluminosilicates, which might have been the original clay minerals in contact with the organisms that were being fossilized (Butterfield 1990a). The presence of large numbers of burrowing creatures and algae suggests that the Burgess Shale fossils lived in shallow-water muds within the photic zone.

The range of fossils is so large that we do not have the space to describe them here. They are nicely described in several books and papers (Conway Morris 1998; Gould 1989; Whittington 1985; Whittington and Conway Morris 1985) and are introduced and illustrated in excellent photographs in Briggs et al. (1994). One must first remember that fossils typical of the Cambrian – trilobites, brachiopods, and hyoliths – are found in abundance, as they are also found in coeval deposits in the region of Canada and the United States. But the Burgess Shale teaches a sobering lesson about what is normally missing in the fossil record. The soft-bodied fossils comprise the majority of the biota and give us a depressingly clear idea of what is missing from most muddy-bottom fossil deposits. In soft bottoms, we would expect a variety of burrowing and surface grazing invertebrates; these are found in abundance in the Burgess Shale. They include a diversity of the now-depauperate priapulids, an abundant acorn worm–like fossil, a variety of polychaete annelids, the velvet worm *Aysheaia,* and the enigmatic *Wiwaxia,* which must have lived on, and foraged along, the sediment surface. A large fauna of surface-dwelling arthropods was also found, many members of which could not be placed in obvious conventional arthropod categories (Briggs and Fortey 1989; Whittington and Conway Morris 1985). Especially of interest was the trilobite *Naraoia,* which consisted only of two shields (unlike the normal trilobite three) and lacked a calcified dorsal exoskeleton. Perhaps *Naraoia* is an ancestral trilobite; this might figure importantly in linking the Cambrian trilobites with possible Precambrian forms yet to be discovered (see below).

The Cambrian Diversity Trap

The earliest stages of the Cambrian, the Manykaian and the Tommotian, are distinguished by their peculiar shelly fossil fauna (see discussion in Bengtson 1977, 1992). A diverse array of problematica includes small conelike shells, the conularids, single valves, the so-called *Mobergella* fauna, and even exquisitely preserved embryos and their small hatchlings (Bengtson and Zhao 1997), which are segmented and perhaps juvenile halkyriids. This diversity of weird organisms led Bengtson (1977) to suggest that the Cambrian was a period of evolutionary creativity. Extinction of many groups led to the residual group of phyla that we see in extant faunas. This hypothesis was more or less repeated later by S. J. Gould (1989) as the "Wonderful Life hypothesis," with the additional suggestion (totally untestable, but fun) that a replay of the "tape of life" would result in a different outcome; our extant fauna might just as well have been dominated by descendants of conularids, for example.

The sense of high Cambrian diversity at high taxonomic levels also infiltrated the field of paleontology through two developments in paleontological analysis during the 1970s and 1980s. Because they were well preserved in some Cambrian and Ordovician rocks, echinoderms were classified into a large number of higher taxa, and eventually there were 21 named taxonomic classes of the phylum Echinodermata, which was quite an increase from the 10 living and extinct classes to be found in Hyman (1955). In the Cambrian, 9 classes were named. After a dip in diversity in the Late Cambrian, probably owing to poor preservation (Smith 1988), the Ordovician experienced a resurgence of echinoderm diversification with 14 recognized classes, with a steady subsequent decline later in the Paleozoic (Sprinkle and Guensburg 1997). This conception of echinoderm evolution only reinforced the idea of early class-level diversity, culminated by culling to the present-day mere 5 extant classes.

Oddly enough, this interpretation of echinoderm evolution happened with no fanfare. The standard treatment in the *Treatise on Invertebrate Paleontology* (Moore and Teichert 1978) described various Cambrian echinoderm fossils that had no obvious affinities to the extant classes. The practice of the time, which was largely based on phenetic association, was to "reward" such differences with a new taxon of high taxonomic level. Thus, the Cambrian and Ordovician came to be populated with a large number of echinoderm forms, some oddballs, of class status. Among these are the celebrated Cambrian carpoids, whose morphology was likened to that of chordates (Jefferies, Brown, and Daley 1996), although this hypothesis has been met with widespread skepticism (e.g., Gans and Northcutt 1983; Peterson 1995). These developments produced a group of subphyla or classes with no obvious hierarchical structure.

The effect of this class-level approach was to create a series of higher-level taxa with no apparent roots – an "evolutionary lawn," whose shoots could not be related to each other and whose origins were perhaps polyphyletic.

The next confirmation of early higher taxon richness arose from an extremely important reexamination of the Burgess Shale, supervised by Harry Whittington, who came to occupy the Woodwardian Chair at Cambridge, a worthy successor to Adam Sedgwick. With his students Simon Conway Morris and Derek Briggs, Whittington recollected and restudied the Burgess Shale fauna. In truth, C. D. Walcott had done only a preliminary study on the entire fauna; he did not get to the stage of doing monographic descriptions, including careful morphological study and taxonomic assessment. The new study was much more careful in examining characters of certain taxa that might have had novel taxonomic significance.

The new "Cambridge Campaign" (Conway Morris 1998) moved the Burgess Shale vision of the Cambrian in the direction of the evolutionary lawn concept, previously inspired by the plethora of echinoderm classes. Conway Morris (1977) discovered a distinct new wormlike organism with seven pairs of spines and tentacles. Its consummate weirdness led to its name: *Hallucigenia.* It was portrayed as propped on the bottom by the seven pairs of spines, with tentacles protruding upward (Figure 8.5), which might make sense if the tentacles were armed with poisonous defensive compounds. In any event, its presence suggested that species with no close affinities to extant phyla were to be found in the Burgess Shale. Other taxa only confirmed the impression of the weirdness of Burgess Shale creatures. Walcott first described *Wiwaxia corrugata* as a polychaete annelid, with scales that he likened to the elytra that covered the dorsal surface of scale worms, such as those found in the polychaete family Polynoidae. Conway Morris reexamined *W. corrugata* and published a careful and extensive monograph (1985) that claimed that *Wiwaxia* revealed a new phylum, perhaps related to the mollusks (Figure 8.6). Conway Morris was impressed with the broad ventral surface, which could be likened to the creeping surface of mollusks (like the shell-less aplacophorans), contained a jaw, and lacked the ventral sclerites expected of a polychaete.

These new taxa and their supposedly profound differences were the cornerstone of Gould's book (1989) *Wonderful Life,* which argued that the weird taxa were part of a menagerie of morphologically disparate phyla that could not be related to extant taxa. Although Gould offered no real morphological or cladistic analysis, he extolled the discoveries and heroic interpretations of Whittington, Briggs, and Conway Morris as

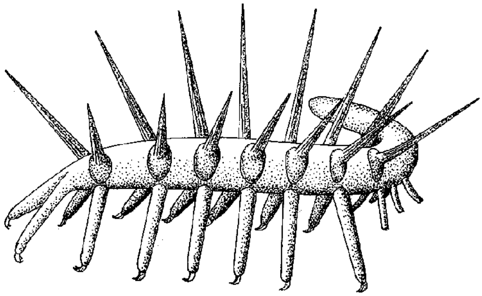

Figure 8.5. The enigmatic fossil *Hallucigenia,* whose oddball status has been reduced to membership in the lobopods, relatives of the extant velvet worms.

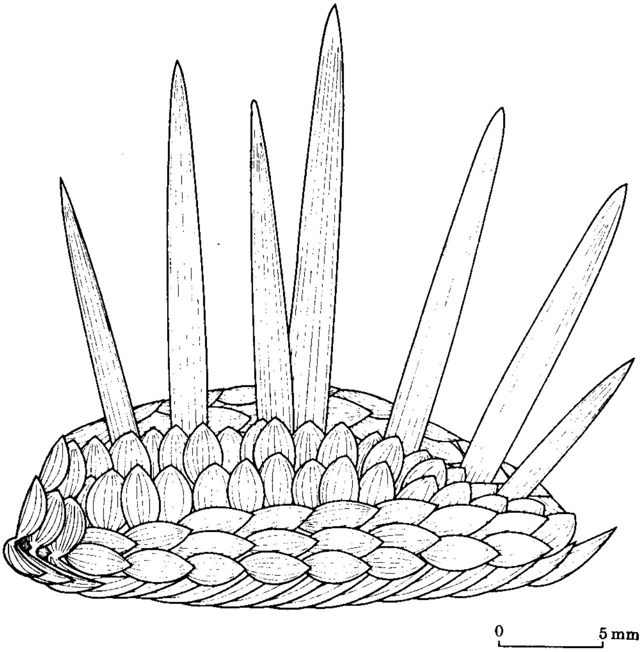

Figure 8.6. Reconstruction of *Wiwaxia corrugata,* a member of a Cambrian invertebrate group with no clear membership in any extant phylum. (From Conway Morris 1985, with permission.)

a reflection of the burst of phylum-level evolution in the Early Cambrian, that was followed by a burst of extinction, leading to the residual of phyla that we know today.

Higher Categories Come First

The next and perhaps most important fact about the Cambrian, won from years of intense collecting, is that all but one of the preservable marine phyla appear in the Cambrian. When I was an undergraduate stratigraphic paleontology student, I had a pile of index cards with fossil ranges, many of which started with Ordovician. No longer true! Cambrian origin applies also to the class level, although the Ordovician has to be added to complete the bulk of the modern story. As discussed in chapter 2, the geological range of the Bivalvia has steadily been extended backward and its lower range now extends to the Early Cambrian. The Bryozoa still stubbornly refuse to be found in the Cambrian, but I suspect that it is a matter of time and collecting luck. What follows from this is an even more interesting fact: Hardly any phyla have their first appearance after the Cambrian. This was stated first by George Gaylord Simpson (1944) as the generality that "higher categories come first." The meaning of this is clear: So-called higher categories are indicative of basic morphological differences, and the appearance of these differences is concentrated near the beginning of an evolutionary radiation. Cloud (1948) argued similarly that "evolutionary eruptions" were marked by a high occurrence of variability, perhaps caused by high mutation rates. Some might argue that phyla are hardly hard and fast entities. Earlier splits might be biased in favor of higher-level taxonomic rank. Maybe so, but I think it is fair to say that the basic higher-level status of most invertebrate phyla found in the fossil record existed by the end of the nineteenth century, but our sense of the dictum that phyla come first in the fossil record did not develop until much later. Thus, some notion of fundamental differences – baupläne, if you will – arose before we knew that it all began in the Cambrian. This "fact" figures importantly in our conception of the Cambrian as the beginning of it all.

Recapitulation: The Cambrian Catechism

The story told thus far has led to a picture of the Cambrian that involves a novel time of creativity, rapid divergences, production of many phyla that fail to make it to the present day. Here are the talking points:

1. *When?* All modern animal phyla diverged as the fossils indicate, in the second two stages of the Cambrian, or perhaps as far back as the latest Vendian.
2. *Are they all here?* Many phyla erupted in this radiation, but perhaps most did not survive, even beyond the Early Cambrian, to the present day.
3. *Only then?* This creative period was unmatched later; no new phyla appeared, despite subsequent environmental change and major mass extinctions.

Some other points bear mentioning. Although it is true that shelly fossils mark the base of the Cambrian, and the subsequent Tommotian fauna is marked by skeletal phyla such as arthropods and brachiopods, soft-bodied forms clearly also participate in the radiation. Bioturbation is clearly in evidence just below the Cambrian boundary, as is a proliferation of trace fossils (Grotzinger et al. 1995). Furthermore, the Lower Cambrian Burgess Shale–like fossils include a large group of soft-bodied forms. Thus, the radiation may be characterized perhaps as a rise in large-bodied triploblasts, but not as a sudden appearance of mineral skeletonized fossils. We are now finding Vendian calcified tube-dwelling forms in any event (e.g. Grotzinger et al. 1998). In addition, the Cambrian boundary marks an apparent radiation in acanthomorphic acritarchs, a widespread group of spiny planktonic fossils presumably members of the eukaryotic phytoplankton (Butterfield 1997). This radiation may comprise a trophic link to the rise of large numbers of large-size benthic animals, which depend on vertical transport for their food supply, perhaps accelerated by newly arisen zooplankton via fecal pellets (Butterfield 1997; Levinton 1996).

"Oddballs from the Cambrian Start to Get Even"

The witty title of Bengtson's (1991) article (reproduced in the above heading) aptly describes the fate of the "ain't that weird!" school of Cambrian paleontology, exemplified by Gould's 1989 popular book. Indeed, as the book came out, it was already becoming clear that many of the presumed phylogenetic outliers were far more enmeshed in a more prosaic framework of evolutionary relationships. *Hallucigenia*'s status as a wild and new creature bit the dust just about as Gould's book came to be read. This realization was only part of the many discoveries that evolved from the Late Atdabanian rocks of Chengjiang in southern China, whose fossils had been discovered over 50 years ago but whose significance was not appreciated until restudy in the 1980s (Hou, Ramskøld, and Bergstrom 1991). A large fauna of Early Cambrian fossils strongly resembled those of the Burgess Shale but set back in time the origins of many groups. Most importantly, a fauna of wormlike creatures known as lobopods demonstrated that the velvetworms and allies were diverse in the Cambrian (Ramskøld and Xianguang 1991). The lobopods (Figure 8.7) were distinguished by a series of paired armored plates and the Chinese discoveries made sense of other fossils, such as the Baltic *Xenusion. Hallucigenia* was just a member of this clade, and it had been reconstructed upside down to boot! These findings demonstrated that like the priapulids, a presently rare group could have had an earlier time of higher diversity. The lobopods were merely an extinct group on the ancestral part of the tree that included the more derived Onychophora.

The lobopods and allies had a number of characters that clearly allied them with the arthropods but placed them in an ancestral position in the larger arthropod clade. To establish even more perspective, an important contribution by Wills, Briggs, and Fortey (1994) examined all of the arthropods by means of a careful character analysis and demonstrated that the Cambrian arthropods were not a helter-skelter group of taxa with no apparent interrelationships. Rather, they comprised a well-structured clade. There were some interesting surprises. The Trilobitomorpha turned out to be the most derived group of arthropods. This is intriguing, if only because trilobites appear fully formed in the first animal-rich Cambrian deposits, which makes one wonder where all of the ancestral forms were hiding! Previous arthropod bizarre outliers, such as the Burgess Shale *Odaraia,* with enormous eyes and valves, fit safely within the Crustaceanomorpha. And so on. It was a fascinating clade with tremendous diversity, but hardly an evolutionary lawn.

A fairly similar fate awaited the spiny weirdo *Wiwaxia corrugata.* Recall that Walcott had identified this worm as a polychaete, perhaps allied with scale worms. Nicholas Butterfield, who pioneered acid washing as a preparatory technique for the Burgess Shale, was able to discern fine structures in exquisite detail. Butterfield (1990b) found tiny sclerites associated with *Wiwaxia* that resembled the presumed neurochaetae of the Burgess polychaete *Canadia.* This suggests an annelid association for *W. corrugata.* The story is far from settled, however, as *Wiwaxia* has the previously mentioned jaw and ventral surface that appears to ally it with the mollusks and perhaps a group known as the halkyerids. Conway Morris (1985, 1989) argued an affinity of *Wiwaxia* with mollusks but agreed that it is most likely a stem lineage annelid. Conway Morris, however, reserved the halkyerids for a more totipotent position in the history of the animals. The halkyerids can be related to *Wiwaxia* readily because of a similar arrangement of medial, dorsal, and ventral hollow sclerites. *Wiwaxia*'s dorsal sclerites are elongate and all sclerites are unmineralized, but this may be the evolutionary outcome of rather minor character transformations from analogous (perhaps homologous?) characters in the halkyerids

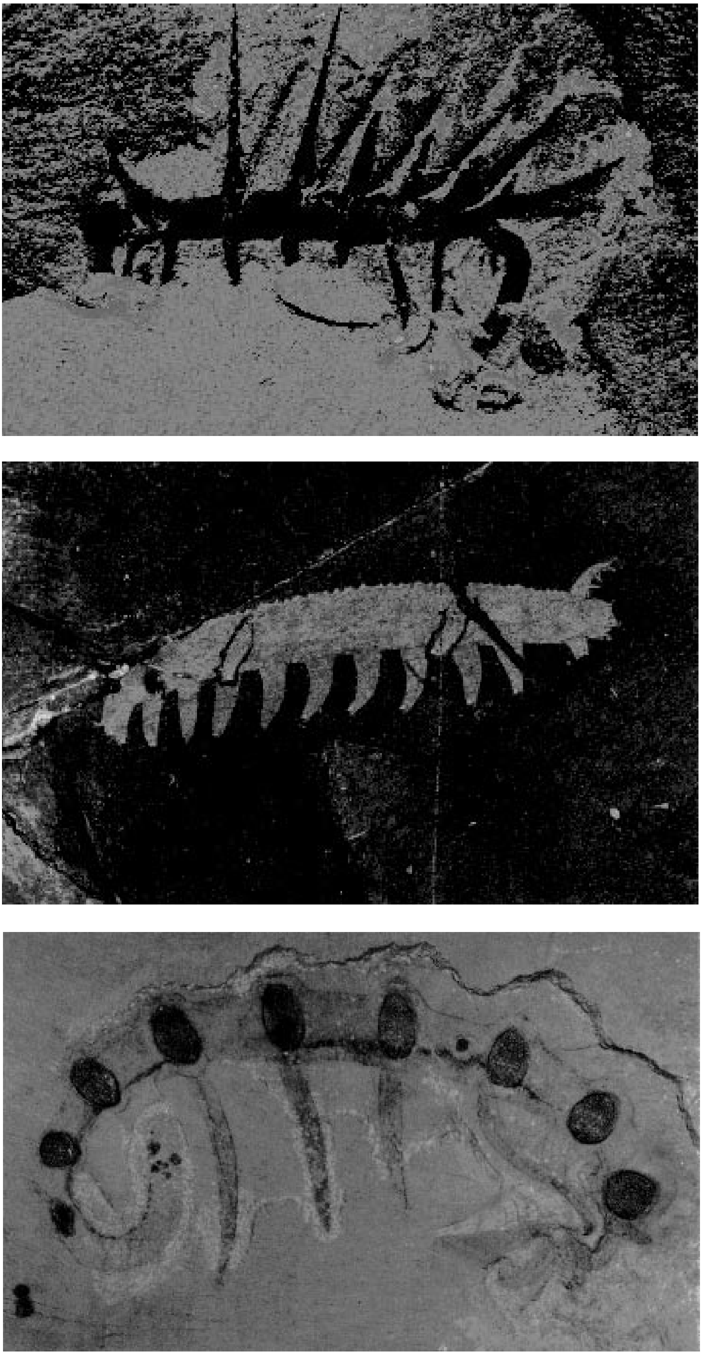

Figure 8.7. Lobopods found in the Cambrian. Top: *Hallucigenia sparsa* from the Middle Cambrian Burgess Shale; middle: *Aysheaia pedunculata,* Burgess Shale; bottom: *Microdictyon sinicum* from the Lower Cambrian Chengjiang Formation, south China. (Top and middle from Briggs et al. 1994, photographed by Chip Clark, with permission from the Smithsonian Institution. Bottom from Conway Morris 1998, with permission.)

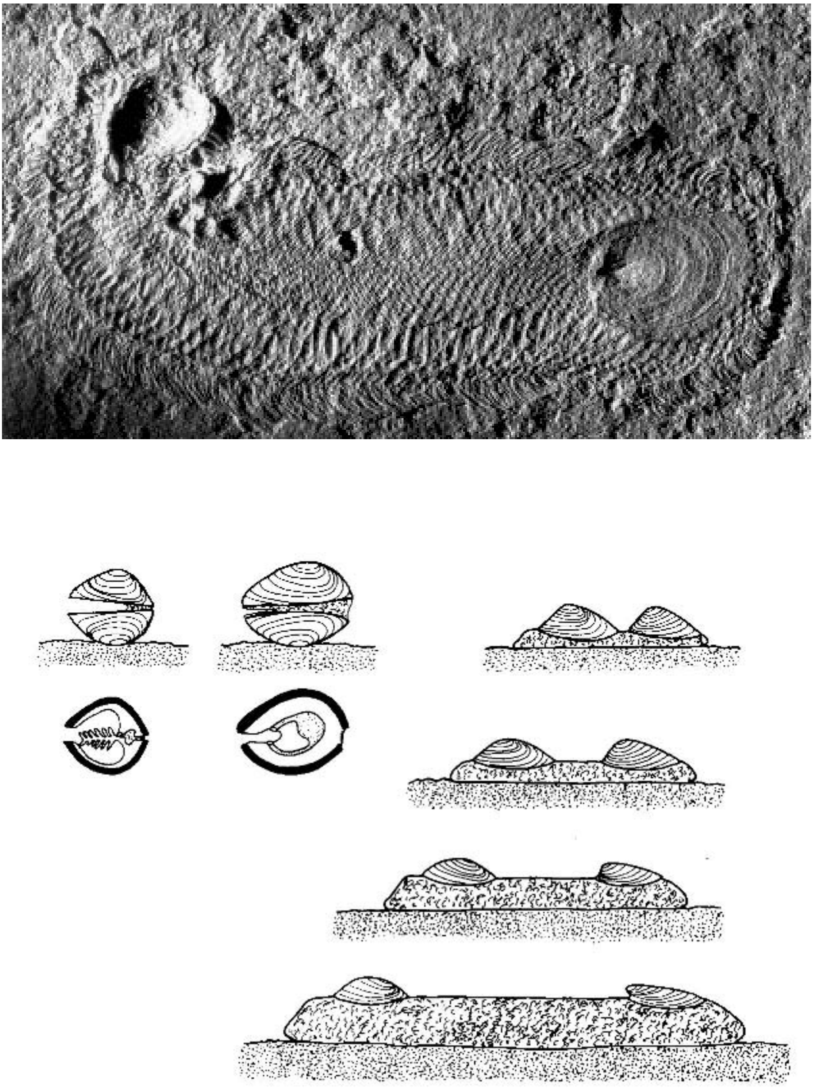

Figure 8.8. Top: a halkyerid from the Sirius Passet site in Greenland; bottom: a set of hypothetical transitions from halkyerids to brachiopods. (From Conway Morris 1998, with permission of Oxford University Press.)

(Figure 8.8). The remarkable halkyerid found in the Greenland Sirius Passet site has an anterior and a posterior dorsal shield, each of which resembles a brachiopod shell. Does this mean that this halkyerid is related to brachiopods? Possibly, and this figures in an interesting, if speculative, evolutionary tree argued by Conway Morris (Figure 8.9). My own intuition simply cannot make the leap from separated "valves" to a brachiopod, but current evidence is too sketchy to exclude many hypotheses.

Finally, we return to the "lawn" of echinoderms. The total of 21 classes, with no apparent cladistic structure, was reexamined by Paul and Smith (1984) and by Smith

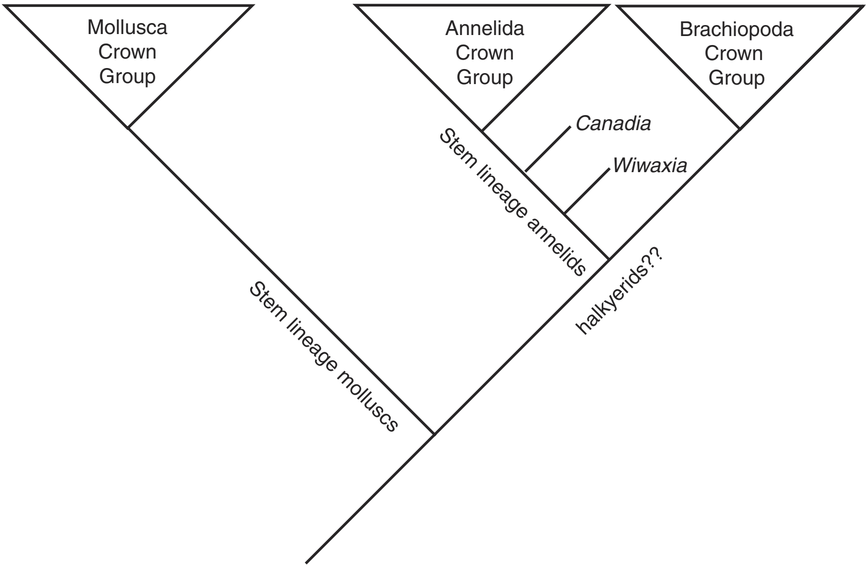

Figure 8.9. Tentative cladogram of three of the protostome animal phyla, emphasizing the position of some stem groups. (Modified from Conway Morris 1998, with permission.)

(1984). Smith (1984) pointed out the lack of information content of older classifications of the Echinodermata, which emphasize the larger subphylum structure with no character analysis. In effect, this approach (e.g., Moore and Teichert 1978) creates the impression of an evolutionary lawn, simply by ignoring the characters that might impart evolutionary structure. As mentioned above, there is a reward for emphasizing difference by recognition of higher-level taxa, which plays into the hands of hypotheses that emphasize the disparity of early Paleozoic fossil groups.

Studies emphasizing character analysis, however, paint a very different picture (Paul and Smith 1984; Smith 1984). For example, both embryological and fossil characters agree in uniting the brittle stars and the asteroid starfish. The eocrinoids can be shown to be a group united more by ancestral character states than by shared derived characters; this makes for confusion, and Smith (1984) demonstrated that they are not a monophyletic group. They are instead probably a hodgepodge of taxa, ancestral to several lines of more derived and monophyletic echinoderm groups. In many cases, ancestral echinoderms have a set of traits that cannot be used to define membership in living or more derived groups. For example, the Cambrian helicoplacoid *Helicoplacus gilberti* is very generalized and its characters allow membership in only the stem group of the entire Echinodermata. Figure 8.10 shows how all of the fossil groups of echinoderms can be assigned to the stem group of one of the crown groups defined by extant forms. Of particular interest is the fossil genus *Camptostroma*, formerly considered to be the only representative of the class Camptostromatoidea. It possesses all of the autapomorphies of crown-group echinoderms but lacks the autapomorphies of either the Pelmatozoa or Eleutherozoa. It therefore defines a three-taxon polytomy (Figure 8.10), defining a group in which the latest ancestor of crown-group echinoderms would be placed (Paul and Smith 1984; Smith 1984).

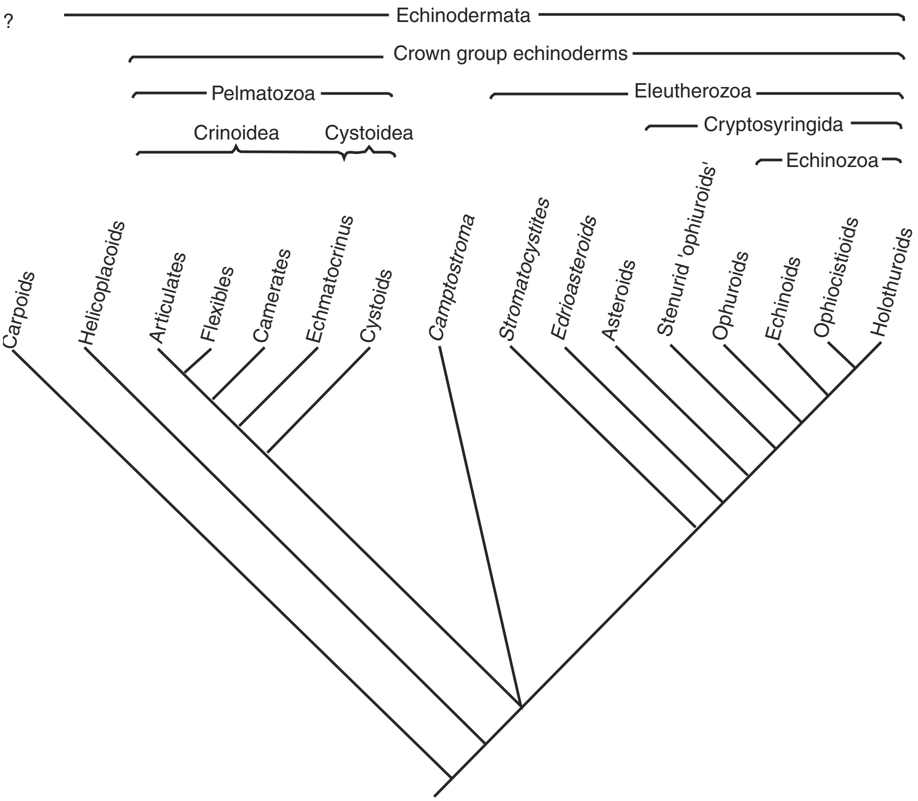

Figure 8.10. Cladogram of the important groups of echinoderms. All fossil groups can be assigned to a stem group of one of the crown groups. (Modified from Smith 1984, with permission of the Palaeontological Association.)

The echinoderm cladogram, based on a careful character analysis, defines a straightforward evolutionary tree, not a lawn, although questions still remain unresolved (Littlewood, Smith, Clough, and Emson 1997). With this analysis, the oddballs continue to become even, kind of like 1960s hippies becoming stockbrokers.

The trend continues. Until the advent of molecular sequence techniques, it was often difficult to establish relationships among apparently distantly related groups; this falsely highlights the multiple weirdo–evolutionary lawn hypothesis. No set of groups has been more victimized by this shortcoming than the "wormy" groups, set into phyla such as the Annelida, Echiura, and Pogonophora. Oddly enough, it was the discovery of the giant vestimentiferan tube worms that set a revision of this story in motion. The vestimentiferans were discovered next to deep-sea hot vents and later near colder water hydrocarbon seeps. They are worms often exceeding 1 meter in length and are the fastest-growing invertebrates in the world (Lutz et al. 1994). At first, they were accorded phylum status, but careful examination of the morphology of early developmental stages showed that they were most likely highly specialized pogonophorans (Jones and Gardiner 1989; Southward 1988). The plot thickened when molecular evidence from several studies characterized pogonophorans as derived annelids and vestimentiferans as members of the Pogonophora (Black et al.

1997; McHugh 1997; Winnepenninckx, Backeljau, and Wachter 1995). The status of the Echiura is still unsure; they may be derived annelids or perhaps a sister group of the annelids. In either event, another lawn has turned into a tree.

The result of this analysis argues strongly against the evolutionary lawn–Cambrian weirdo hypothesis. Indeed, it casts strong doubt on the notion of a Cambrian period of heightened evolutionary creativity of many new phyla and classes, most of which who subsequently disappeared. The Cambrian was a time of radiation, no doubt. Indeed, if the fossil appearances are to be believed, the Cambrian explosion is genuine, at least with regard to the appearance of a large number of new groups. But it is hardly the inverted cone of either taxonomic diversity or morphological disparity that has been argued by Gould (1989). Instead, the Cambrian shows a gradual unfolding of groups as they radiated, leading to an eventual radiation of our modern crown groups, often by the later Cambrian or Ordovician. This trend can be seen in echinoderms (Smith 1988), arthropods (Walossek and Müller 1989), and other groups. Gould's point of view is more of an expression of ignorance of the practice of systematics and a mistaken impression of the Cambrian fossil record. Perhaps we should better term this period "wonderful life, writ ordinary"?

Morphological disparity maximized in the Cambrian explosion? The notion of a Cambrian Explosion implies that a period of evolutionary eruption might have produced a peak of morphological difference among taxa, as a presumably ecologically driven radiation expanded taxa into many new ecological roles. The evolutionary lawn metaphor, combined with a proliferation of naming of higher taxa, only reinforces the vision of a Cambrian cornucopia of disparate forms. The argument would be completed by stating that subsequent times experience a winnowing of these major taxa, which results in a reduction of morphological disparity in today's biota. The echinoderm story mentioned above fits well with such a model.

Has disparity peaked in the Cambrian, and has it declined ever since? This was one of Gould's (1989) main arguments. If we fix on groups such as the velvetworms or priapulids, we do get a sense of decline, because these are minor phyla of low present-day morphological diversity. Later evaluations of morphological disparity, however, do not suggest a decline at all. Briggs, Fortey, and Wills (1992) used multivariate techniques to examine disparity in Cambrian and living arthropods and found no difference in level of overall morphological disparity. This result was robust, arising either from phenetic or cladistic analyses. They argue that previous conceptions of high Cambrian disparity related more to artifacts of naming of taxa, rather than by genuine differences in morphological disparity. Problematic taxa were more an artifact of inadequate taxonomy than a result of more disparate Cambrian groups. Recently, Loren Smith and Bruce Lieberman (1999) examined the radiation of olenelloid trilobites to see if morphological change declined with increasing time during the radiation. But transition distances did not decline with rank or age, which suggests that the tempo of morphological evolution did not decline with rank in tree or with advancing time.

Combined with the cladistic reconsiderations of "class proliferation," these results suggest that the Cambrian might have been the beginning, but it was not a special time of morphological explosion disproportional to those of other times.

So what was special about the Cambrian? Most importantly, it might have been the source of our modern fauna. Given the number of living animal phyla, a relatively small number of species, perhaps all alive in the Early Cambrian, must have given rise to the fauna we observe today. We are no closer now than we were decades ago, however, in understanding whether this small number of lineages was determined by ecological circumstances arising in the Early Cambrian or whether they were survivors of an earlier Precambrian divergence in either the Vendian or much before.

We also are yet to understand whether the sudden appearance of trilobites, brachiopods, and even fishes in the Lower Cambrian was truly the beginning. We can say, however, that the Cambrian was likely a time of steady radiation, which can be seen especially well in trilobites (Smith and Lieberman 1999) and echinoderms (Smith 1988). These Smith Brothers have helped to dispel the idea of a Cambrian cough, which was followed by a precipitous wheeze of diversity.

Gould tears down Walcott: A scientific morality saga. There is a regrettable aspect to this entire story, so get ready here for a diversion. Gould (1989) co-opted Whittington's hypothesis to develop what he saw as a radically new hypothesis of the nature of evolution. The Cambrian biota was taken to be a diverse series of familiar forms along with many oddballs, whose phylogenetic relationships were distant, reflecting a rapid radiation that resembled a sprouting lawn, whose visible shoots could not be related to each other in the roots below ground. This led to the notion of an inverted cone; the Cambrian had been a wellspring of phylogenetic diversity of groups whose relationships were distant and unfathomable. Thus, the fauna of today is a happenstance group of survivors that might have been completely different if a different chance selection had occurred.

Gould's book (1989) denigrated Charles D. Walcott's achievements, to the point of characterizing even his monumental fieldwork as not worthy of extraordinary recognition. This view, to say the least, is not shared by anyone else (see Yochelson 1996), much less the subsequent stars of Burgess Shale inquiries (Conway Morris 1998; Whittington 1985). I have to admit that when I read Gould's book, this peculiar treatment of Walcott was a shock.

Gould saw Walcott's identifications of Burgess Shale fossils as a failure to recognize their fundamentally bizarre nature and blamed this failure on the various administrative duties that diverted Walcott from discovering the truth. Walcott's wartime duties did restrict his time, and he characterized much of his Burgess Shale studies as preliminary, but not many professors with lines of students at the door, meetings to attend, and courses to teach would have been diverted much less or would have achieved nearly as much. Indeed, how many professors do you know who have carried out 60,000 fossils from any locality, even on the side of a freeway? I know a couple, and they are the superstars of the breed. But let's not get too upset about this, as Gould is eager not so much to tear Walcott down as to make him a character in a sort of morality play of scholarship. Trapped by your times and distractions, you will fail to see a novel truth.

Gould (1989) also saw Walcott as shackled by the chains of systematic convention; why else did Walcott fail to see that many of his fossils were weird animals, soon to be caged and curated properly in the menagerie of *Wonderful Life*? Well, to put it simply, Walcott did *not* do so badly. Yes, he screwed up the reconstruction of that wonderful predator *Anomalocaris* and shunted off some of its body parts into the wrong phyla. But I assert that you, the reader, would likely have done as badly.[4] Walcott classified the very enigmatic *Wiwaxia* as a polychaete, resembling a sea mouse. To this day, that hypothesis stands strongly, alongside quite different interpretations (Butterfield 1990b; Conway Morris 1985). *Eldonia* was thought to be a holothurian, and Gould leapt on it as another oddball, but a reanalysis still keeps Walcott's interpretation alive (Yochelson 1996).

Walcott also failed to see that the worm *Aysheaia* was an onychophoran, but so did a contemporary expert (Clark 1915). The person who discovered *Aysheaia*'s velvetworm affinities, G. Evelyn Hutchinson (1931), was, ironically, well tutored in traditional arthropod zoology, having been in classes given by Borradaile at Cambridge and keeping his notebooks for references in his own lectures at Yale University, at least into the 1960s! Indeed, this traditional education allowed him to spot the enormity of Howard Sanders's discovery in the 1950s of specimens of what Sanders was soon to describe as the Cephalocarida, a new subclass of Crustacea.[5]

One can go on like this, but the picture is clear. Walcott identified fossils the way you or I are liable to do: He tried to ally them with groups already identified. He got lots right and correctly recognized that others were unusual and assigned them to new families (although he kept to a standard contemporary higher-level classification, as any field paleontologist would be likely to do). Others he missed, but that is a hazard of identifying an entire fauna with so many species. His was not a formal systematic monograph but a description of a fossil fauna, as Yochelson (1996) aptly pointed out.

As a strong form of poetic justice, Gould's perorations about bizarre unrelated forms came back to haunt him. As discussed above, many of the weirdest fossil species, including the not so aptly named *Hallucigenia,* were later found to be members of a rather clearly related clade, the lobopods, related to the modern velvetworms. Indeed, the work that paved the road to this conclusion (Ramskøld and Xianguang 1991) succeeded because of modern methods of character analysis and cladistic work that had been employed to establish phylogenetic relationships. Such an approach has been absent completely from Gould's analysis or discourse over the years. Personally, I think that is one strong reason why he missed the boat so badly.

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[4] I have a favorite mentor who described eight species of invertebrates, only to be embarrassed by a later worker, who found them articulated as a chiton!

[5] In my graduate classes in the 1960s, I remember Hutchinson still actively engaged in his discovery of the true affinities of *Aysheaia.*

Precambrian Whisperings of the Rise of Animal Life?

Molecules to the rescue? The relationship of molecular divergence to time has been likened to the ticking of a clock, which might be used to date important moments in evolutionary history such as the divergence of the animals. Unfortunately, as divergence time reaches the level of hundreds of millions of years, several problematic biases creep in. First, not many DNA sequences evolve slowly enough such that given nucleotide sites do not change more than once, which can erase the evolutionary signal. Multiple hits will fog the degree of divergence by allowing the degree of sequence difference with time to reach a plateau where more change does not give more information. Sequence divergence, combined with other processes such as deletions and other rearrangements, also leads to difficulties in aligning sequences of distantly related taxa.

Ever since the idea of a molecular clock has been proposed (Zuckerkandl and Pauling 1965) we have hoped to be able to estimate times of evolutionary divergence. A random process of substitution is implicit in clock models, which implies that a poisson distribution (variance of substitution rate equals the mean estimated rate) should fit the data (Ohta and Kimura 1971). This model often does not fit the data. As Cutler (2000) notes, there are four typical ways of dealing with this problem:

1. Don't ask, don't tell
2. Shopping for molecules that fit the assumptions
3. Shopping for taxa that fit the assumptions
4. Using models that correct for the usual overdispersion of rates

In order to use many loci in an analysis, investigators are forced to use option one. Any sort of selection to satisfy the random model will greatly reduce the number of molecules or taxa to be employed. For example, the study of Ayala et al. (1998) goes to the extreme of removing about two thirds of the taxa in some cases to achieve a fit This would call into question the value of ignoring most of the data, for the sake of forcing the small remainder into a particular model. Cutler (2000) strongly recommends option four and devises a test with maximum likelihood as the basis for calculating relative degrees of confidence.

A final and profound problem with using molecular data to date the divergence of the major animal groups is the need to extrapolate from a group of divergences that are calibrated by known fossil data. It is obvious that we cannot use divergence times of the major animal groups themselves, so we must resort to using divergences among fossil groups that are more recent, whose living representatives are also available for DNA sequencing. Given the uneven preservation of the record, we are confined to using milestones in the fossil record of readily fossilizable groups such as vertebrates, mollusks, brachiopods, and echinoderms. In these cases, one could find a number of divergence times for which there is good fossil evidence and hopefully DNA sequences for appropriate genes (e.g., Wray, Levinton, and Shapiro 1996). Furthermore, sequences are uneven in coverage, and the over-the-transom approach often fails to produce sequences for some sister groups that are well documented paleontologically. Very few genes will have enough taxonomic spread to give us a good calibration spanning the history of the calibrating data set (e.g., vertebrate divergences). As an alternative, one might use a single calibration date for one well-understood splitting time, reasonably well justified by the fossil record (e.g., tetrapods versus ray-fin fishes-Wang et al. 1999). One might be able to get data for many genes for such a set of taxa. The disadvantage lies in total dependence on one or very few calibrating dates.

First of all, sister taxa must be reckoned, and the earliest occurrence of one of the two taxa is then taken as the time of divergence, even though it is possible that the time might be quite a bit deeper (Smith 1994, Sanderson 1997). This source of error is especially a problem in studies in which one uses only a very few fossil calibration points (e.g., Doolittle et al. 1996; Lynch 1999). It is less a problem when many fossil divergence times are used (e.g. Runnegar 1982), as a regression between time of divergence and sequence difference can be calculated. One does worry, though, about extrapolating such a calibration from a single group such as vertebrates to a larger number of invertebrate phyla.

The first study, using α- and β-hemoglobin amino acid sequences (Runnegar 1982), proved to be a tantalizing challenge to the Cambrian divergence hypothesis, as invertebrate distances suggested a divergence time of 1 billion years ago, based on the overall relationship between calibration points based on vertebrate fossil divergence times and amino acid sequence difference. The study was attacked vehemently by Erwin (1989), a staunch supporter of the Cambrian Explosion hypothesis, who cited the usual problems in using molecular clocks. Most worrisome was the problem of extrapolation, as the vertebrate relationship had to be extrapolated to the much greater invertebrate genetic distances. It was possible, for example, that the rate of sequence evolution might have been different during a highly divergent episode of animal evolution such as that represented by the putative Cambrian Explosion.

In 1996, Wray, Levinton, and Shapiro did a study quite similar to that of Runnegar's pioneering efforts, but they extended the analysis to six additional sequences, including nuclear and mitochondrial sequences. The study also used a large number of taxa for a calibration using vertebrates, to establish a relationship between genetic distance and divergence time (a correction was made for multiple hits, developed by Kimura 1980). The results revealed much scatter (Figure 8.11) but confirmed the deep Precambrian divergence estimate for the divergence time between protostomes and deuterostomes. Estimates of the protostome–deuterostome split (referred to below as the P–D split) hovered around 1.2 billion years ago, although Wray et al. were clear in pointing out that the scatter precluded any conclusion beyond the inference that the divergence of the animal phyla occurred long before the Cambrian explosion hypothesis would allow. Wray and colleagues noted that the greatest problem in making such estimates is the lack of confidence limits of the regression of genetic distance on divergence time in the vertebrate calibration. They used a couple of conservative means of calculating the confidence limits of the P–D split, and yet these error bars still precluded a Cambrian Explosion hypothesis, either the extremist hypothesis (Gould 1995) or the intermediate explosion hypothesis (Valentine, Erwin, and Jablonski 1996).

One alternative hypothesis that cannot be safely ignored is the possibility that molecular evolution accelerated during the Cambrian Explosion. To conform to the

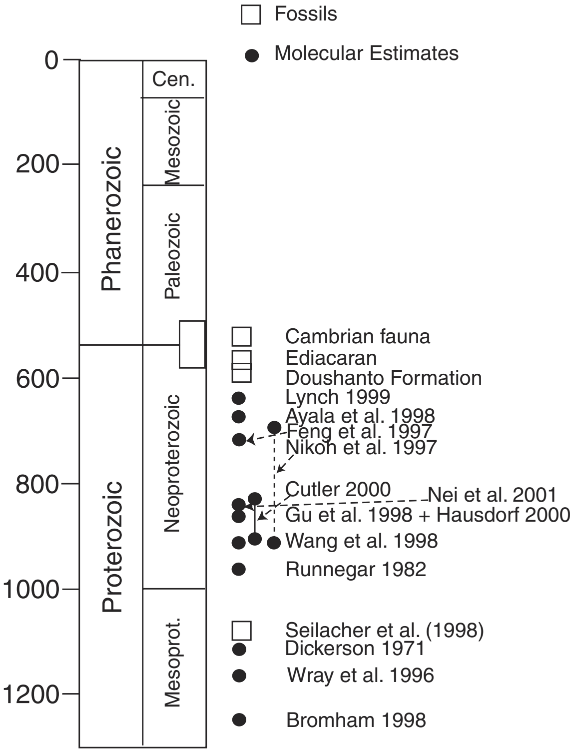

Figure 8.11. Estimates of divergence times of the protostome–deuterostome splits, with some fossil occurrences.

extreme Cambrian Explosion estimate of about 10 million years (Gould 1989; Grotzinger et al. 1995), such an acceleration would have to be by a factor of 65, or by a factor of 10 for the more protracted explosion estimate of about 35 million years (Valentine et al. 1996). Although differences in rates of evolution are well known, this large difference, especially in several genes of unrelated function, including mainly housekeeping genes, would be unprecedented. Even Valentine, Jablonski, and Erwin admitted this. Wray et al.'s data come mainly from amino acid sequences of proteins, and such acceleration would have disastrous functional consequences. Furthermore, Wray et al.'s use of a relative rate test brackets the variation in rates to just a few percent. If one examines the genetic distances in selected genes from nonmetazoan eukaryotes to chordates and compares them with nonmetazoan eukaryotes to protostomes, one finds variation of just a few percent, with no apparent bias in rate difference (Wray et al. 1996). This suggests strongly that there was no such acceleration in molecular substitution rate during a putative Cambrian Explosion.

The problem of early acceleration of substitution rate has recently been studied by Bromham and Hendy (2000), who used multiple calibration dates and a method using empirically determined variation of substitution rates. They found that allowing the substitution rate to be maximal during the basal "interphylum" splits still precludes a Cambrian divergence time for the phyla. As this extreme, the minimum possible divergence time is 586 million years ago.

The Wray et al. study questions the timing of P–D divergence, but what of the explosiveness of it all? The echinoderm–chordate divergence estimate is 172 million years to 224 million years later than the three mean protostome–chordate estimates. Although the exact numbers may be questioned, they suggest that the divergence was protracted and not explosive. Moreover, in six of the seven sequences, we recovered the correct temporal order of the following splits: protostome–deuterostome, echinoderm–chordate, Agnatha–Gnathostomata. Given the wobbly nature of the molecular clock, it seems unlikely that such resolution would be possible if the divergences all occurred within just a few million years, over 500 million years ago.

Since this study, a number of other molecular estimates have all produced Precambrian estimates of the P–D split (Figure 8.11), although most have placed the split closer to 800 million years to 900 million years, as opposed to the 1 billion to 1.2-billion-year estimate of Wray et al. Several of these studies have addressed the problem of rate heterogeneity by dropping cases of significant heterogeneity along different branches of the tree (Bromham, Rambaut, Fortey, Cooper, and Penny 1998; Wang et al. 1999). As an example, Bromham et al. (1998) used a method known as quartets (Rambaut and Bromham 1998) to estimate the time of the P–D divergence. Whole mitochondrial protein-coding sequences as well as 18S rRNA sequences were used. Taxa were grouped into permutations of two pairs of sister taxa. For each pair, genetic distance and divergence time were known, on the basis of fossil data, and those shown to be homogeneous in rate of sequence divergence could be used to estimate the time of splitting of the two sister groups. This approach has the advantage of including many fossil calibrations, as in Wray et al. 1996. A maximum-likelihood approach was used to test and exclude most quartets with significant rate heterogeneity. This approach produces a wide range of estimates, but all are Precambrian and deeper than 680 million years ago. A second recent robust study (Wang et al. 1999) used a more restrictive group of taxa and fossil calibrations but employed a great deal of sequence data to produce an estimate of 942 million years for the arthropod–vertebrate split. Cutler (2000) found a result statistically consistent with Wray, Levinton, and Shapiro (1996) using a Poisson model, but also found that divergence times were inconsistent with this model. Using a model assuming overdispersed divergence rates, he still found a maximum likelihood fit to a Precambrian divergence time for the P–D split, most likely in the confidence range of ca. 824–917 million years. For all seven trees examined, a Cambrian explosion date of 600 million years led to a significantly lower likelihood for the data than the older divergence. Nevertheless, the Cambrian hypothesis (at least of 600 million years divergence time, which Cutler uses for an uncited reason as the base of the Cambrian) still has a good fit, which only further heightens the variability of the data. In sum, the molecular evidence for a Precambrian split between protostomes is overwhelming and consistent. What is not convincing is the exact time; estimates are just too spread out right now to inspire much confidence.

A couple of estimates have placed the P–D split closer to the base of the Cambrian. Ayala et al. (1998) reanalyzed Wray and colleagues' (1996) data and added more, by means of an algorithm that supposedly removes branches of the tree that imply significant heterogeneity in rate. With such an adjustment, they arrived at an estimate of the P–D divergence of 710 million years ago. This is nearly 200 million years before the Cambrian, but they incorrectly saw this as consistent with the Cambrian Explosion. Regrettably, their results cannot be taken too seriously. The algorithm they used removed as much as two thirds of the taxa originally used by Wray et al. (1996), which violates at least my conception of removing outliers of a distribution. Would chopping two thirds of one's body away be considered a therapeutic amputation? Furthermore, their residual group of taxa used for analysis produces no improvement in the heterogeneity of divergence time estimates among genes, relative to that of Wray et al.

Another estimate employed 10 mitochondrial protein-encoding genes (Lynch 1999). The P–D divergence was found to be 630 million years ago. The use of mitochondrial genomes is potentially an important advance in this field, but Lynch's analysis had the fatal shortcoming of using only two benchmarks, one of which is severely questionable. One was the tetrapod–ray-finned fishes split, which was taken to be 430 million years ago. This is probably close, but the split could have been 100 million years before. The troubling one was the fungi–animal split, taken by fossil evidence to be 1,100 million years ago. It is likely that this date could be wildly inaccurate, especially because eukaryotes appeared about 2,000 million years ago (Knoll 1992). Indeed, the fungi–animal calibration is based on an apparent diversification of eukaryotes at 1,200 million years ago to 1,000 million years ago, not any specific useful information about the fungi–animal split. As Knoll (1992, p. 626) noted, this diversification may demonstrate "diversification within a few easily fossilized groups, rather than among all branches in the crown." Knoll also noted how poor the fossil record before 1,000 million years ago really is, casting strong doubts on the use of fossils for molecular calibrations. If the fungi–animal split was much deeper in time than 1,100 million years ago, Lynch's estimate would have to be revised deeper in time. At this time, one has to take this result with very little confidence. As Knoll pointed out (p. 623), the split might have been "substantially earlier." If so, then Lynch's estimate will have to be revised, but only to an earlier time. For example, if the fungi–animal split was 1,500 million years ago, the P–D split would be estimated at 750 million years ago. If the fungi–animal split corresponds more to the time of origin of the appearance of fossil eukaryotes (Knoll 1994a; Knoll and Carroll 1999) at 1,700 million years ago, then the P–D split would be pegged at over 800 million years ago. The molecular estimate of Wang et al. (1999), based on about 50 genes, is 1,500 million years ago to 1,600 million years ago. Unfortunately, Lynch's analysis was not very stable, owing to this problem, but still, taken literally in its current form, it still placed the P–D split about 100 million years before the Cambrian.

There *is* a net trend to all of the analyses. They all refute the estimate that all of the animal divergences occurred at the time of the Early Cambrian. They also refute the estimate of a P–D divergence 30 million years before, as advocated by Valentine and colleagues (1996). They all suggest a deeper time for splitting and a non-explosive spread of divergence times, especially for the bilaterian groups (Wray et al. 1996; Hausdorf 2000). What is discouraging is the tremendous spread of estimates.

Along with time estimates, construction of trees should illuminate our inferences about the divergence of the animal phyla. Unfortunately, not many sequences have proven useful, because rate of divergence is usually too rapid to be useful for resolution of splits in such deep time. Philippe, Chenuil, and Adoutte (1994) examined 18S rRNA sequences from 15 animal phyla and were not able to resolve triploblasts very well at all. They inferred that the multifurcations found are compatible with a Cambrian Explosion hypothesis and that the explosion must have occurred within 40 million years. Unfortunately, this conclusion is clouded by the strong rate heterogeneity among sites. Abouheif, Zardoya, and Meyer (1998) showed that among-site rate variation was more likely the explanation for the poor resolution of the 18S rRNA phylogeny. Indeed, when they removed some of the more variable sites, much more resolution was found within the deuterostomes, although the protostomes remained unresolved. The combination of a deep split and rate variation probably preclude the use of 18S rRNA as a useful tool for such deep resolution, although generalities such as major groupings within the animals (Aguinaldo et al. 1997) and the monophyly of some phyla can be determined by use of this sequence and others (McHugh 1997). Lynch (1999) noted that the rapid production of mtDNA genomes for many species provide hope for developing accurate phylogenies.

The results of Wray et al. (1996) show that even protein-encoding genes may yield a reasonable phylogeny, which would be a surprise if the major radiations occurred in just a few million years. We can calculate from the data a probability of getting the correct order of appearances (protostome→deuterostome; echinoderm→ chordate; agnathan→gnathostome) from the seven sequences (Table 8.1). An assumption of independence of estimates among genes yields a probability of getting the correct order of 0.00016. If rates of the mitochondrial genes are correlated owing to linkage, but the nuclear genes are independent of each other, and of the mitochondrial genes, then the probability of the order found for the different divergences is 0.0348. This latter assumption is overly conservative, because great spans of time would tend to reveal differences related more to difference in substitution rate among the genes, which are considerable.

Given the vagaries of the molecular clock, we would not expect to get a correct order of appearance if the animal phyla diverged in just a few million years, as is suggested by the Early Cambrian fossil record calibrated by radioisotopic estimates. Levinton and others (in preparation) simulated both evolutionary trees and nucleotide sequences and found that it is unlikely that any correct resolution of a tree would be possible under a strict Cambrian Explosion scenario. Indeed, their evidence suggests that the divergence of the animal phyla likely occurred over a protracted period, possibly greater than 100 million years, which fits our molecular results.

If the invertebrates diverged around 1 billion years ago, then they are in good company. At this time, there is evidence for a major radiation of the eukaryotes. The Mesoproterozoic–Neoproterozoic boundary (1,000 million years ago) marks the diversification of the red, green, and chromophytic algae (Knoll 1994a). Molecular phylogenies suggest that this was part of a broader radiation of “higher” eukaryotic phyla. Observed diversity levels for protistan microfossils increased significantly at this time, as did turnover rates. The next period of protistan microfossil diversification was near the base of the Cambrian. Thus, the 1-billion-year mark, or perhaps a few hundred million years before (Cavalier-Smith 1991), might have been the glori-

Table 8.1. Rank Order of Divergence Times for Estimates of Animal Phyla Divergences in Wray et al. (1996)

	ATPase 6	Cytochrome C	COI	COII	Hemoglobin	NADH	18S rRNA
Gene type	Mitochondrial	Nuclear	Mitochondrial	Mitochondrial	Nuclear	Mitochondrial	Nuclear
Protostome–deuterostome	3	3	3	3	3	3	3
Echinoderm–chordate	2	1	2	2	2	2	2
Agnathan–gnathostomata	1	2	1	1	nd	1	nd
Probability	0.167	0.833	0.167	0.167	0.5	0.167	0.5

With 3 divergence times, there are 6 permutations, whereas with 2 estimates, there are just 2 permutations. In the case of cytochrome C, the probability is 1 – [probability of correct sequence of three divergences].

COI = Cytochrome oxidase I; COII = Cytochrome oxidase II; NADH = reduced form of nicotinamide adenine dinucleotide; nd = no data; RRNA = ribosomal RNA.

ous time when all of the divergences of modern eukaryotic groups began, including the animals. This hardly means that groups such as trilobites and brachiopods appeared at this early time fully formed; it means only that the lines leading to these crown groups may be quite ancient.

Morphological and genetic implications of the deep molecular splits. What are the implications of the apparent consistent molecular evidence supporting a Precambrian split, about 800 million years ago to 1,000 million years ago, of the protostome–deuterostome line? Does this mean that we are bound to find a long-overlooked cache of trilobites, brachiopods, and mollusks in billion-year-old rocks? Unlikely! Will we find nautiloids swimming among Precambrian stromatolites? I doubt it. Those who hold the Cambrian as a fount of new large animal phyla, many resembling those of the present, are bound to be vindicated. It is naive to believe that Precambrian splits imply an unpreserved deep Precambrian biota of large-bodied burrowing and epifaunal creatures. For one thing, the lack of vertical burrows much before the upper Vendian precludes this (Budd and Jensen 1998; Grotzinger 1995b; Jensen, Gehling, and Droser 1998)

But it is equally naive to dismiss the evidence for Precambrian divergences as devoid of meaning. Gould (1998) blundered by stating:

> In fact, I don't see that it matters one whit ... whether one worm-like species carrying the ancestry of all later animals, or ten similar worm-like species already representing the lineages of ten subsequent phyla, crossed this great divide from an earlier Precambrian history. The Cambrian explosion embodies a claim for a rapid spurt of anatomical innovation within the animal kingdom, not a statement about times of genealogical divergence. [p. 64]

Let's overlook the fact that Gould (e.g., 1989, p. 310) and others *did* believe that the major splits in the history of triploblastic animal life coincided with the appearance of the fossils!

Of course, forms associated with stem groups are liable to look a bit fuzzy with regard to the characters by which we recognize extant crown groups. But rather than emotive statements, we need an assessment of what character appearances might be associated with what phylogenetic divergences and how these associations influence interpretations of morphological evolution.

Take the protostome–deuterostome divergences, for example. We now have convincing evidence that the split occurred substantially before the Cambrian. Conway Morris (1998, pp. 143–144) intuited that it must have occurred with the appearance of small-bodied forms about 750 million years ago, and molecular evidence points to a somewhat deeper time. We can take the synapomorphies of the protostomes and deuterostomes to reconstruct to some degree what the ancestral triploblastic bilaterian must have been like, even if we cannot conjure up its exact appearance. The following list gives us some idea of these features:

1. *Hox* genes – anteroposterior, dorsoventral axis specification
2. *Engrailed,* specifying segmentation
3. *Dll,* specifying distal structures

4. Muscle-specific MYOD – turns on muscle fate
5. Nervous system
6. Cephalization – *orthodenticles* gene, anterior and regionalized nervous system
7. *Pax-6* – photoreceptors, eye organizer?
8. Rhodopsin
9. Gene *tinman* sets up circulatory system – heart in *Drosophila* and vertebrates
10. Dorsoventral axis specification
11. Lysyloxidase protein, needed for cross-linking of collagen→skeleton (Ohno 1996)

These characters give us the following picture: a bilaterian creature with nervous organization, cephalization, the capability of large body size owing to a circulatory system, and the capability of producing a skeleton owing to the presence of lysyloxidase. In other words, even *this* crude an analysis gives us a bilaterian that can take the form of many of the body plans of the modern animal phyla. DeRobertis and Sasai (1996) suggested that the group encompassing a subset of these traits be named the Urbilateria. This gene set is so deep within the history of the bilateria (Figure 8.12) that we clearly need much more information from the fossil record and perhaps the distribution of more diagnostic developmental genes before we can make definitive statements about potential thresholds in animal evolution (Knoll and Carroll 1999).

At the minimum, the implications of this list toss out some current hypotheses. Clearly, organisms bearing much of the modern *Hox* gene arrangement existed in deep Precambrian time; therefore, the presence of *Hox* genes could not have been the cause of the Cambrian Explosion (Erwin, Valentine, and Jablonski 1997). Similarly, the presence of a nervous system likely long predated and therefore cannot be implicated in stimulating the Cambrian Explosion (Stanley 1992).

We need more molecular information to further refine inferences about the features of Precambrian phyla and their body plans. For example, it would be extremely useful to develop molecular estimates of the divergence times among protostome or deuterostome phyla, respectively. For example, Aguinaldo et al. (1997) have identified a subgroup of protostome phyla, including the arthropods, nematodes, onycophorans, priapulids, kinorhynchs, and tardigrades, that are unified by the presence of a common molting mechanism, ecdysis (Figure 8.12). If so, we can conclude that ecdysis arose just once. Suppose the divergence date for these phyla proves to be deep within the Precambrian. We can then conclude that this morphological innovation is not related to the Cambrian Explosion. The divergence of the lobopods may be interesting and might have set the stage for a Cambrian radiation, but the crucial character of a molting exoskeleton would not have been the stimulus for the radiation. Similarly, a character such as the presence of a radula might be a crucial synapomorphy for much of the molluscan clade. The timing of divergence of the associated taxa would be crucial in judging whether the rise of this character was influenced by a Cambrian trigger or whether the character was already "in the bank," waiting to be used at the right moment to help facilitate the divergence of larger-bodied radula-bearing groups in the Cambrian. The discovery of *Kimberella* (Fedonkin and Waggoner 1997) suggests that radulae might have preceded the Cambrian explosion.

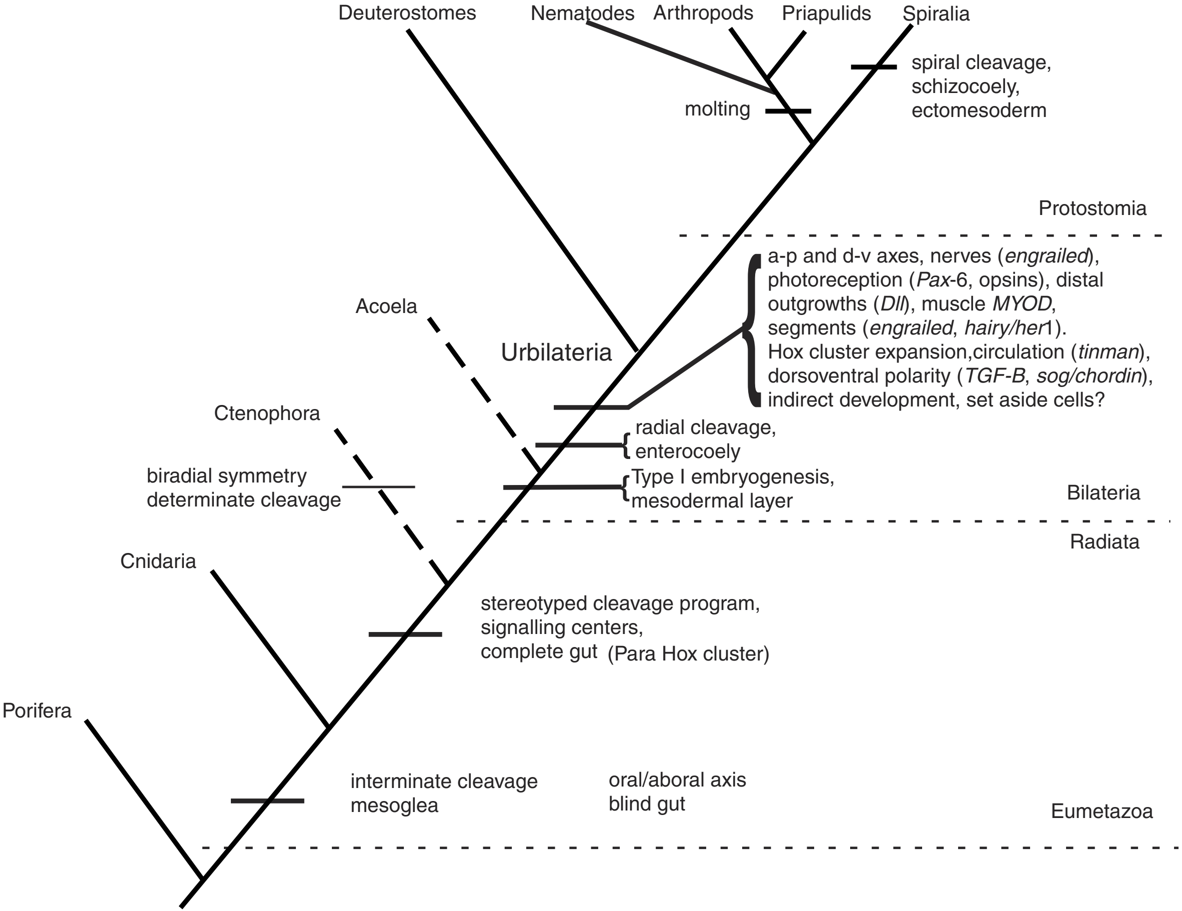

Figure 8.12. Tree depicting major events in the history of animal life. (Modified from Knoll and Carroll 1999, with permission of the American Association for the Advancement of Science.)

Balavoine and Adoutte (1998) pointed out that the support of a division of the protostomes into two monophyletic groups – the molting Ecdysozoa and the Lophotrochozoa – further suggest deep Precambrian origins of major splits within the protostomes. Of greatest interest is the failure of the acoelomate and pseudocoelomate phyla to locate themselves in "primitive" positions on the evolutionary tree (Figure 8.13). The pseudocoelomates do not form a monophyletic group: Rotifers and gastrotrichs are grouped with the lophotrochozoans. Kinorhynchs, priapulids, nematodes, and nematomorphs, however, are grouped with the arthropods in the Ecdysozoa. The acoelomates are found allied with the coelomates. These results make Gould's above-quoted argument about "ten similar worm-like phyla" rather ironic, as it is obvious that he fell into the trap of believing in a ladder of life, with primitive wormy things coming first, followed by the "higher complex forms." This is the very mind-set that he so descried in others. As it turns out, the "primitive" wormy forms are often quite derived. As Balavoine and Adoutte pointed out, the traditional organization of life may be upside down, as the forms thought to be coelomless and therefore primitive are widely scattered and allied with derived

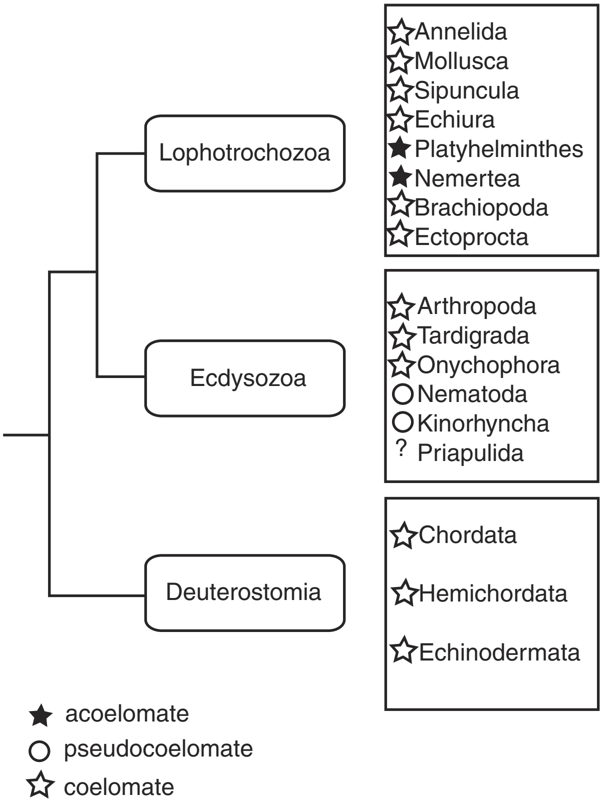

Figure 8.13. Division of triploblastic animals: the Deuterostomia is the sister group of the Lophotrochozoa–Ecdysozoa clade. Note the scattered alliance of acoelomate and pseudocoelomate groups with "higher-grade" animal phyla. (Modified from Balavoine and Adoutte 1998.)

groups. Our new understanding of protostome evolutionary relationships, therefore, opens the possibility that large-bodied coelom-bearing forms or smaller relatives existed in deep Precambrian time.

Precambrian Fossils Reconsidered

Preston Cloud's seminal article convinced us that the Cambrian Explosion might have been much more than an artifact of preservation or just an ecological stimulus that increased body size. Since then, a properly critical eye has been cast on many so-called Precambrian animal fossils, and they have been shown to be sedimentary structures, members of algal groups, or at best unconvincing (Hofmann 1992). And yet, here are the nagging molecular data, asking us to reexamine the situation.

No one doubts the special nature of the Cambrian. Are we likely to find a deep Precambrian and 1-meter-long *Anomalocaris,* "one mean shrimp," as a popular magazine put it? Will we find an *Olenellus* fauna in rocks of a billion years of age? The Cambrian, so beautifully documented by the window Walcott gave us on the Burgess Shale, was clearly a special time when animal life exploded into the wide range of forms that we associate with the modern faunas of today. So what does it mean to find molecular estimates of animal and even within-deuterostome divergences that are so much older? That is the challenge, both to paleontologists and phylogeneticists.

We can imagine three hypotheses that include the possibilities suggested by the molecular data:

1. *Cloudian Cambrian Explosion:* The fossil record as we understand it reflects the divergence of all animal phyla within the Tommotian and Atdabanian stages of the Early Cambrian.
2. *Lost-world hypothesis:* The animal phyla as we know them today (or in the Cambrian) evolved long before the Cambrian, perhaps as far back as 1 billion years ago. Therefore, some day we will find a fossil locality with trilobites and brachiopods, but perhaps in miniaturized form.
3. *Stem-group hypothesis:* The Precambrian molecular divergences exist because there was a deep Precambrian fauna. This fauna, however, is morphologically distinguishable from the Cambrian forms. They have a set of ancestral characters defined by the molecule-dated divergences, along with other apomorphic characters, amounting to a diverse but ancestral fauna.

The molecular data we now have gathered is consistent with the last two hypotheses.

If we take the molecular results seriously, then should paleontologists reconsider their conclusions that true triploblastic metazoans are missing much before the Lower Cambrian? There are several ways to address this.

Are there no fossils? It is not so easy to spin a yarn that connects the Cambrian biota in a continuous chain to our putative point of triploblastic animal origins of 750 million years ago to 1,000 million years ago. A number of fossil finds now suggest that our search image for Precambrian fossils might have misled us.

Taphonomic considerations now suggest that we will not find many instances of Ediacaran-like preservation in the Cambrian, even if the typical Ediacaran animals had lived at the time. Bioturbation would have readily destroyed the special circumstances under which such fossils would have been preserved, as influenced by the presence of microbial mats. In the same manner, we can cast backward and ask the likelihood of Burgess Shale–style preservation before the Cambrian. More recently than the Lower Cambrian, there is a surprising dearth of Burgess Shale–style preservation of organic remains, which are limited perhaps to some lacustrine deposits and perhaps the organic walls of some graptolite-bearing mudstones. Butterfield (1995) argued persuasively that this type of preservation was not unique to the Cambrian but nevertheless cannot be found in older rocks that are younger than the Late Riphean, about 750 million years to 850 million years ago. Thus, there is a broad window of time within which animals might have flourished, but we are bereft of a means to observe them. The style of organic preservation in the Late Riphean is similar to that of the Early Cambrian, so one might argue that here is where Burgess Shale–style fossils should be found, or perhaps even in rocks as old as those from 950 million years ago.

These older rocks have not as yet revealed obvious animal fossils. Sun (1986) reported a series of putative animal fossils from rocks from 900 million years to 700 million years ago in the Huainan District, Anhui, China, and allied them with living annelids. The fossils are black, membranous, carbonaceous remains of various elongate and annulated organisms. It is likely that several of these are algae; they certainly are not reminiscent of annelid segmentation. *Pararenicola* and *Protoarenicola,* however, appear to be worms with elongate, cylindrical, and flexible bodies with annulation and even a differentiated bulbous end (Sun 1986; Sun 1994). Even Cloud (1986) could not dismiss these fossils and declared them to be possible annelids, but ones that required much further study. He dismissed most of Sun's other claimed animal finds as nonanimal, possibly algal, in origin. Also, Butterfield, Knoll, and Swett et al. (1994) failed to find animal remains in rocks from Spitsbergen (Svalbard) of similar age with similar exquisite preservation of organic films.

Other search images, however, have revealed some fascinating new finds. Early diagenetic phosphatization may be a crucial window that will reveal Precambrian animal fossils, for such a form of preservation can retain exquisite three-dimensional detail and is found commonly in Precambrian rocks. Phosphatization can preserve delicate organic structures within days of death (Briggs, Kear, Martill, and Wilby 1993). Bengtson and Zhao (1997) reported a spectacular find of globular Lower Cambrian fossils from Siberia and China that were clearly a developmental series from the egg, through several division cycles, to embryos and hatched juveniles. *Olivooides* appears to develop into a hatchling that is annulated and conical, with a round cross section (Figure 8.14). It is reminiscent of coronate scyphozoans, although not enough characters are resolved yet for a definitive analysis. The other fossil, *Markuelia,* develops into a worm that is rolled neatly within an embryonic envelope. The worm appears to be segmented, but its affinities otherwise are unknown. The embryos may be halkyerid, but this is not yet confirmed, as no halkyerids have been found preserved with the embryos.

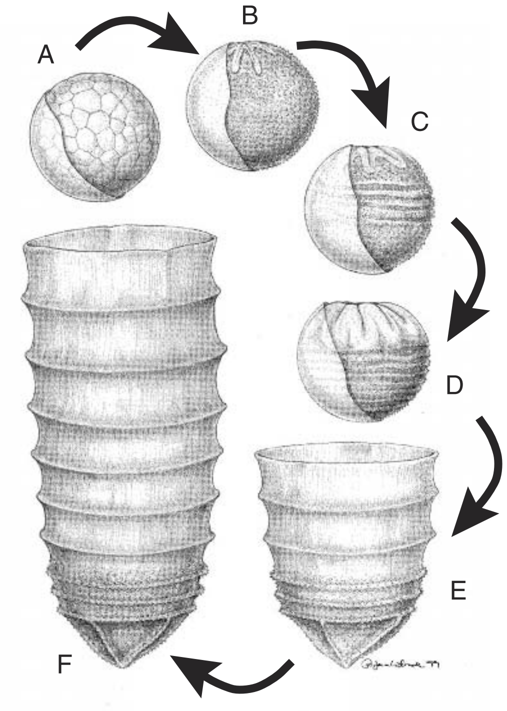

Figure 8.14. A developmental series of *Olivooides* ranging from (**A**) cleavage embryo to (**E**) newly hatched and (**F**) grown specimens. Reprinted from *Embryonic and Post-embryonic Development of the Early Cambrian Cnidarian* (Olivoodes) by Yue and Bengtson from *Lethaia,* www.tandf.no/leth, 1999, 32:181–195, by permission of Taylor & Francis. Figure drawn by Pollyanna von Knorring.)

This form of preservation has been pursued in older rocks, and likely cleavage stages of protostome embryos have been found in the Doushantuo Formation (570 million years ago ± 20 million years) by Xiao et al. (1998). The embryos are all approximately 0.5 millimeter in diameter, with specimens of two, four, eight, and more cells (Figure 8.15). The similar size of all stages strongly suggests an embryo, and the tetrahedral arrangement of cleavage in the four-cell stage suggests a protostome, but possibly a sponge. This exciting development, alas, lacks a corresponding adult, but very little material has been examined thus far. At the least, this is the first direct evidence of bilaterians well before the Cambrian. In the same formation, tiny sponges have been found, including a probable shoe-shaped parenchymella sponge larva (Li, Chen, and Hua 1998). Again, the extension of the range of animals, albeit not bilaterians, has been spread to 50 million to 60 million years before the Cambrian.

These fossils are just tantalizing beginnings. Now that the power of phosphatization as a mode of Precambrian preservation is known, the search will only intensify. This is good, whether or not we extend the range of the protostome and deuterostome Animalia significantly before the Vendian. At least we are looking in a new way.

At the time of this writing, surely the most tantalizing fossil was reported by Seilacher et al. (1998) from the Mesoproterozoic Chorhat Sandstone in India (ca. 1 billion years ago). These appear to be worm trails on weathered bedding planes, interpreted as grazing trails on the sediment surface, beneath a microbial mat. The

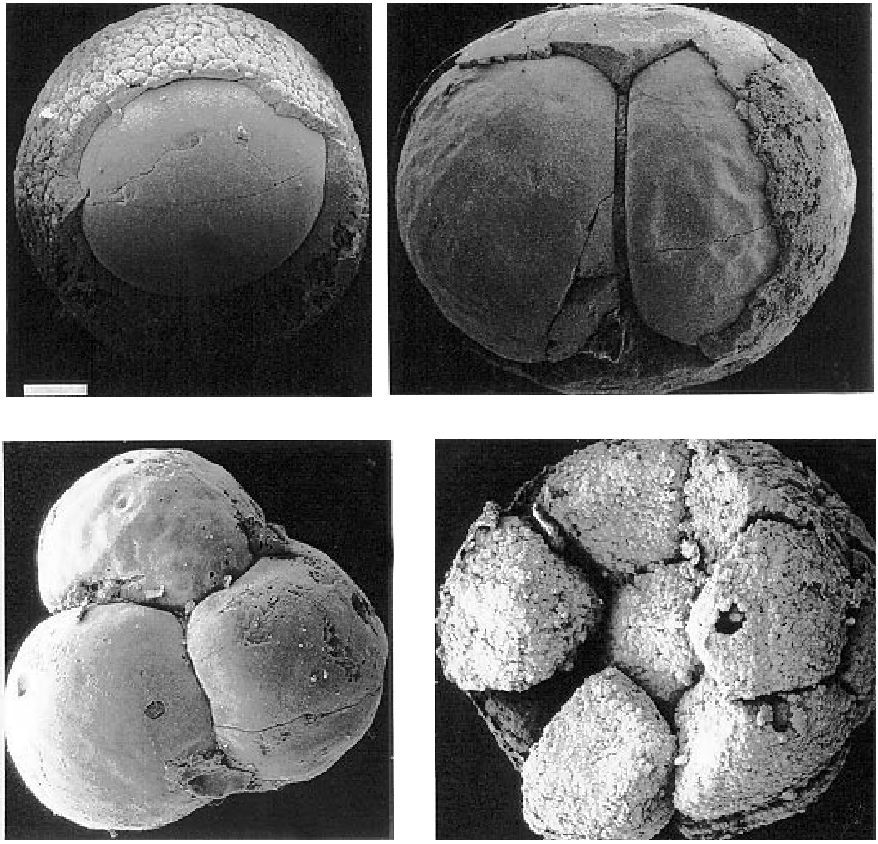

Figure 8.15. Putative fossils of animal embryos from the Doushantuo Formation (570 million years) of China. (Adapted from Xiao, Zhang, and Knoll 1998, with permission from *Nature*.)

shape of the burrows is a bit irregular, but there are ridges of sand on either side of the burrow, suggesting plowing of sediment as the worm moved along. Because the burrows are several centimeters long and a few millimeters wide, we would be dealing with a likely triploblast with a hydraulic skeleton. It may be that such weathered sandstone surfaces bear more examination, but one does wonder why no such burrows have been discovered as yet in rocks between 1 billion years ago and the upper Vendian. Nevertheless, this discovery is very exciting indeed. As of the writing of this chapter, the age of the site is under debate, and even the provenance of the fossil is not generally agreed on.

The recent discoveries should excite paleontologists to start looking intensively for fossils in these previously poorly investigated modes of preservation and to look in other rock and facies types that have been neglected. One must remember that the Burgess Shale was discovered only by accident and relatively recently. It would be unfair to state that there has been a totally inadequate search for Precambrian fossils, but it is equally fair to say that the quest for Precambrian animal life is far from over. The fact that a fish could have been found so recently in well-studied Lower

Cambrian rocks of China (Shu et al. 1999) is an indication that much more will emerge in the coming years.

So Why Not More, Where Are They, and Where Did They Come From?

First, we can consider the possibility that preservation before the Cambrian is inadequate to the task of finding our primordial animal antecedents. Satisfactory explanations in this vein must account for why the fossils have not been found and perhaps where a new search image might produce new fossils. Second, it would be worth a reexamination of some of the Precambrian fossils previously claimed to be triploblasts to see if perhaps they are worth exhuming and subjecting to another necropsy.

Could we find an ancient Precambrian animal fossil at all? A preservational bias hypothesis would argue that some aspect of animal form might preclude its preservation or that the facies appropriate for preservation of the fossils are missing. We discussed above Butterfield's (1995) argument that a large missing time gap in Burgess Shale–like preservation might obscure the rise of the animal phyla between a time of about 750 million years ago and the Cambrian. It is also possible that Precambrian triploblasts were too small to be likely to be preserved as body fossils and that they also left no traces, given that large-bodied creatures with hydraulic skeletons were absent. This hypothesis conforms to notions of the origins of the protostomes and deuterostomes as planktonic larval-like forms, bearing the essences of protostome and deuterostome characters (e.g., Nielsen 1994, 1998). These two groups would have arisen from a radial gastraealike ancestor. Being on the order of a few hundred microns in size at most and soft bodied, such fossils would likely never have been preserved, even if they had an array of morphologies specialized to planktonic and benthic life. I have to admit that the larval-small-size hypothesis is a bit of a cop-out. It safely excludes Precambrian failure of preservation from observational scrutiny. But there it is; it just might be true. It has a venerable history: Ernst Haeckel first conceived of the gastraea as the ancestor of all eumetazoans.

Davidson, Peterson, and Cameron (1995) proposed a developmental constraint that might explain the presence of a diverse but small-body-size Precambrian menagerie. Larvae of many invertebrate species have complete guts and swim and feed in the plankton. Before settlement and metamorphosis, a series of "set-aside" cells develop within the larva that often are the source of the cells that give rise to the entire adult, which develops on metamorphosis. The larval cells by contrast are a developmentally restricted set that, by this hypothesis, cannot give rise to the typical structures we see in large-body-size bilaterians. Thus, the advent of set-aside cells would permit a Cambrian explosion. For this hypothesis to be tenable, one would have to prove that set-aside cells indeed are ubiquitous in indirect developing species (i.e., those with larvae and complete metamorphosis) and that genes specifying spatial organization in adults (i.e., *Hox* genes and others) are not active in larvae. Confirming this, a strong dominance of expression of *Hox* genes has been found in imaginal-type tissue in late-stage larvae of the urchin *Strongylocentrotus purpuratus* (which forms the cells of the adult), but only two of the eight studied

Hox genes show any activity in the early larva (Arenas-Mena, Martinez, Cameron, and Davidson 1998). The lophotrochozoan polychaete *Chaetopterus* sp. apparently does not have Hox gene expression in early embryos but expression is found very early in larval development before any trace of segmentation is found. The expression suggests that polychaetes have representative genes of each of the Hox cognate groups except Abd-B (Irvine et al 1997; Peterson et al. 2000). The expression is localized to the region of teloblasts, but it is not exactly clear that the expression is confined to a true and distinct set-aside cells region. The result is intriguing but awaits further exact study of cell fate.

This hypothesis would require that set-aside cells and the *Hox* body-patterning genes predated the P–D split. It also would require an explanation of arthropods, which do not have indirect larval development. One impediment to this hypothesis is the discovery that the Acoela, once thought to be members of the Platyhelminthes (flatworms), have been reevaluated as the most ancestral bilaterians, on the basis of an 18S rDNA evolutionary tree (Ruiz-Trillo, Riutort, and Littlewood 1999). Although this group superficially resembles other flatworms, a number of embryological features also set it aside from the phylum. It is triploblastic with a spiral cleavage form that is distinct from other spiralian phyla. Most importantly for the Davidson et al. hypothesis, the acoels do not have planktonic larvae, suggesting that there is nothing special about the sudden rise of an adult capable of large body size. Speculation in this direction has only been heightened by the exciting discovery of a strong similarity and perhaps homology between internally fertilized filiform sperm of flatworms, ancestrally positioned annelids, and in the Neomeniomorpha, a group of worm-like aplacophorans (Buckland-Nicks and Scheltema 1995). These results may further suggest a weakness of the hypothesis that ancestral bilaterians arose from free-spawning organisms with planktotrophic larvae, let alone with set-aside cells. More information is now being developed by Peterson and colleagues on larval versus adult developmental gene expression, especially in basal deuterostomes (e.g., Peterson, Cameron, Tagawa, Satoh, and Davidson 1999; Peterson, Harada, Cameron, and Davidson, 1999b).

The "small and fuzzy" hypothesis seems to include the necessity of the animals having vague morphologies that are unspecialized and bearing no resemblance to the features of the modern animal phyla. As such, some might argue that even if such forms existed, it might be sophistry, therefore, to use the molecular data to deny that there was a Cambrian explosion of animals, in the sense of origin and divergence of the modern animal body plans, in a concentrated period of time. I dealt with this hypothesis above and concluded that the molecular evidence suggests a primordial animal that was equipped to be a typical bilaterally symmetrical organism with a complete nervous system and complete gut. It is entirely reasonable that these forms are members of plesions with a set of ancestral characters and a few more that denote one or more stem groups that became extinct. A good model for such a phylogenetic architecture would be Farrell's (1998) analysis of the beetles. A more derived set of repeated radiations in the Cretaceous and later was associated with several origins of different angiosperm groups. But this radiation was long preceded by a primitive radiation of pre-angiosperm insect groups associated with cycads and conifers. Clearly this early group consists of proper beetles, but with primitive features associated with an environment that existed long before the angiosperms, in the same way that small ancestral but well formed animals might have long preceded the Cambrian crown groups.

Consider this additional possibility: The small animals that are not preserved in extant Precambrian outcrops were a reasonably faithful duplicate of modern animal types. A simple possibility might be that all of the animal phyla were represented by interstitial (Boaden 1989) or very small burrowing forms, on the order of 1 millimeter and less in size (requiring the collateral hypothesis that the Cambrian "explosion" was a revolution in size increase and not morphological diversification). Small-animal-body fossils are simply quite rare in the fossil record. We have no good record of harpacticoids or any other copepods, for example, let alone fossils of interstitial polychaetes. Consider a beach on the island of Sylt in the North Sea, studied recently by a consortium of German systematists, who have identified 652 species of animals (Armonies and Reise 2000). With a rarefaction approach, it is believed that a complete recovery would surpass 850 species. It is fair to state that not a single one of these species, no matter how abundant, is likely to be preserved as a fossil. Small body size greatly accelerates the rate of degradation, and the lack of obvious tracks and burrows would exterminate all traces of even a large and diverse fauna. Such is the prospect for recovering Precambrian animal fossils if they are small in body size.

It might be argued that such a "phantom meiofauna" scenario is unlikely, because meiofaunal characteristics are often highly derived, meaning that these groups could not have arisen until more "normal" triploblastic ancestors existed (e.g., with indirect development, which is usually regarded as the ancestral state, relative to lecithotrophic or direct development). Indeed, some characteristics of invertebrates require large body size (Budd and Jensen 1998). But this would be true only if the primordial miniature fauna were confined to interstitial movements among sand grains. If they lived in mud, small body size would be expectable, especially if the food base was scarce and oxygen was in short supply. Such a miniature fauna would also be possible if animals lived in an environment simply not found commonly at the present time. The list of taxa (Table 8.2) includes free-living flatworms and most interestingly nematodes, which are both very abundant in soft sediments. Nematodes may be small, but their free-living representatives are abundant in soft sediments and have a wide diversity of jaw types (Brusca and Brusca 1990).

For example, Seilacher et al. (1998) argued that small metazoans might have lived and foraged at the interface between the sediment surface, but beneath thin algal films or mats. This environment might have disappeared in the Cambrian, during a revolution in body size of burrowing creatures, which would have destroyed previously widespread algal sediment–surface mats. Small annelids (e.g. naids), burrowing a scant 2 millimeters or so below the sediment–water interface, might not have disturbed many bed forms and yet are segmented, much like larger annelids, yet they are triploblastic and have a coelom.

It may be that some shared evolutionary derived characters require some modification of this scenario, at least for some groups. For example, consider the case in which

Table 8.2. Overall Composition of the 652 Animal Species Found on the North Sea Island of Sylt

Faunal Group	Percent of Total Species
Free-living flatworms	32
Nematodes	27
Ciliates	11
Copepods	10
Gastrotrichs	7
Nine other major taxa	13

From Armonies and Reise 1999, with permission.

two closely related phyla or classes share features that require a large body size. It would follow that the common ancestor should be of large body size as well. Small body size would inevitably preclude the development of elaborate gills, large-scale oxygen transporting circulation systems, and so on. It is difficult, for example, to imagine animals smaller than a few millimeters long with a radula although members of the Aplacophora can be less than one mm long. Thus, this trait, if it is the defining synapomorphy of the gastropod–chiton clade, could only have been acquired if body size were of the proportions that would be preservable as fossils. The fossil, however, might be soft-bodied, which would require special circumstances for preservation. It may be that *Kimberella* is just that fossil (Fedonkin and Waggoner 1997).

Perhaps the last breath that can inflate the small-body-size hypothesis comes from some of the known evolutionary relationships of the major phyla, whose sister groups are often unskeletonized and of very small body size (Fortey et al. 1996). For example, the basal sister groups of the rest of the phylum Mollusca are the Aplacophora, especially the Caudofoveata, small wormlike molluscan forms with some peculiar features, such as a possible chitin cuticle. A cladistic analysis of these two groups confirms their basal status (Brusca and Brusca 1990). Similarly, the sister group of the arthropods is the diminutive tartigrades. Maybe one shouldn't get too excited about it, but this at least suggests that the ancestral stocks of some of our known Cambrian dominant phyla could have borne traits that are complex but plesiomorphic.

And Did They Come Only Once?

Cloud (1968) reckoned that the animals arose polyphyletically. This perception would only be heightened by various scenarios that derive the animal phyla from a set of planktonic larval-like forms, which in turn derive from protozoan-like ancestors. If you examine the differences in protostome and deuterostome ciliary beating patterns, you can easily reach the conclusion of a diphyletic origin from several ancestral lines (Nielsen 1994).

One would hope that molecular data would produce a convincing phylogeny that would resolve these problems, but the answer is still voiced without strong conviction. As mentioned above, the antiquity of the splits makes it difficult to find an ideal set of molecules whose nucleotide divergence rates are homogeneous enough or of the exact rate. In attending a symposium on such problems, I was impressed at how bad any particular analysis was statistically, yet if one flipped through the many studies like a pad of cartoons, some general patterns emerged. At present, they all lean toward monophyly.

Although one of the first major papers analyzing 18S rDNA sequences suggested a diphyletic structure for the animals (Field et al. 1988), other studies convincingly suggest monophyly (Lake 1990; Müller, Müller, Rinkevich, and Gamulin 1995; Schram 1991). Currently evidence supports a P–D split, and a division of the protostomes into the Ecdysozoa (nematodes, arthropods, and other molting animals) and the Lophotrochozoa (annelids, mollusks, lophophorates), with overall support for monophyly of the protostomes and deuterostomes, respectively (Aguinaldo et al. 1997; Balavoine and Adoutte 1998). In any analysis, the strength of these inferences is often muted by poor support for one tree, relative to alternative hypotheses. As mentioned above, the entire P–D line's monophyly is supported by the presence of a large number of genes that are not found outside the protostomes and deuterostomes in some cases, or, in others, not outside those plus the cnidarians and sponges. The cnidarians appear to be connected to a more P–D descendant line by *Hox* genes, some of which probably duplicated (Martinez, Bridge, Masuda-Nakagawa, and Cartwright 1998). The *Hox* genes of cnidarians such as hydroids may prove to serve similar developmental roles of setting of developmental gene cascades (Cartwright, Browsher, and Buss 1999). Finally, *Hox* genes have been found in sponges, and Degnan, Degnan, Andrew, and Morse (1995) argued that this demonstrates the monophyly of the Metazoa. As we approach the "beginning," however, it may be harder and harder to find *Hox* sequences, which might be too different in sequence to encounter easily. Thus, the sponges, cnidarian, and P–D lines may constitute a monophyletic group, but from where did they arise? Alternatively, a set of protozoan groups might all have had *Hox* genes and might have given rise to these three great lines polyphyletically. Admittedly, one might have to resort to arguments of convergence, but *Hox* genes appear already to be used and reused for different functions.

Given the fossils, the bottom line is this: The sponges may be sister group of the cnidarians and perhaps the ctenophores. The connections are dubious thus far. The sponges and cnidarians at one end might form an ancestral group, from which the modern animal groups emerged. On the other end of the timeline, we have the emergence of representatives of many living phyla in the Cambrian and Ordovician. There are tantalizing indications of ancestral forms in many of these phyla, especially among the arthropods and echinoderms. But beyond this, the connections between the ancestors and the living phyla are too sketchy to inspire much confidence about any scenario of origins. All we know is that many appear in the Cambrian "fully formed," as if there is a hidden record. But what is that record?

If the modern phyla arose from small ancestors reminiscent of larvae (Nielsen 1994) and were incapable at first of elaborating large-bodied adults (Peterson, Cameron, and Davidson 1997), then we have no block to placing the divergence of major branches of the animal kingdom before the Cambrian. Indeed, if the P–D line is a sister group of the Cnidaria, it is fairly easy to imagine small protostomes or deuterostomes with ancestral traits coexisting with cnidarians in an as yet to be found deposit. But if *Hox* genes or other possibly diagnostic traits prove to ally protozoa with these groups, then there are essentially no constraints on origins. Protozoan form is enormous, and it is not hard to imagine multicellular animals of radial and bilateral symmetry arising from them. A planktonic protozoan *Ctenoctophrys chattoni* has a surprising resemblance to ctenophores (e.g., Weill 1946, cited in Conway Morris 1998). Although the resemblance could be a simple matter of convergence, it is clear that the search for Precambrian fossils is not enough. More attention should be paid to living protistan forms that may prove to be allied with multicellular animals in surprising ways.

What Was the Cambrian Explosion, and What Did Cause It?

Even if animal life diverged significantly before the Cambrian, we are still left with the question of why large-bodied animals diverged so remarkably in such an apparent short period of time. Two classes of hypotheses can be conjured. First, the *environmental stimulus hypothesis* would argue that the animal groups were a loaded gun that was fired on stimulation by a major facilitating environmental change, such as nutrient enrichment or atmospheric oxygen increase. Second, the *key innovation hypothesis* would argue that the acquisition of a major biological feature, be it a developmental gene or a skeleton, facilitated the sudden divergence of many animal groups. The rise of such a key innovation could have been in response to some biological process such as predation, or it could have simply been in response to the appearance of a mutant that bore a character necessary and sufficient for radiation (e.g., a responsive nervous system).

Environmental stimuli. If we wish to come up with an environmental change that might have triggered the Cambrian Explosion, we of course must provide some target date. But the arguments cited above cast considerable doubt on looking for a major trigger at the beginning of the Tommotian.

The events leading up to the Cambrian suggest major environmental changes that might have had great influence on the rise of the animals. During the time encompassed by the later Vendian, perhaps peaking at 700 million years ago, the continental blocks were in a state of assembly, which might have created an opportunity for strong seasonal fluctuations in climate (Valentine and Moores 1971). This age marks the appearance of glaciers as a major influence of planetary climate. A first glaciation occurred around 750 million years ago. At around 580 million years ago, the widespread occurrence of tillites suggests the presence of worldwide glaciation (Knoll 1994b). The probable occurrence of tillites located near the equator may suggest an earth completely covered by ice. This would entail extremely sluggish water motion and reduced carbon dioxide in the atmosphere, which would further cool the earth into a “snowball” world (Kirschvink 1992). Oxygen levels might also have been severely reduced, which is suggested by the appearance of banded iron formations, which form more readily in a very low oxygen atmosphere. Reduced oxygen levels might have been accompanied by lower oceanic pH, under the influence of submarine volcanic emissions.

It is possible that the end of glaciation was marked by enhanced oceanic circulation and upwelling. Late Proterozoic and Cambrian rocks are dramatically enriched in phosphorites, which may be a reflection of nutrient input (Cook and Shergold 1984). Carbon 13 (^{13}C) enrichment in 600-million-year-old rocks may reflect a large-scale increase of atmospheric oxygen (Derry, Kaufman, and Jacobsen 1992; Knoll, Hayes, Kaufman, Swett, and Lambert 1986), but a preceding drop in ^{13}C may also reflect a reduction of atmospheric carbon dioxide and a subsequent reduction of greenhouse warming, thus facilitating glaciation (Kaufman, Knoll, and Narbonne 1997). Continental breakup began by 540 million years ago, which might have allowed oceanic currents to dominate and ameliorate climate. The beginning of the Cambrian also coincided with an apparent dramatic rotation of the earth's upper crust and a consequent latitudinal drift of the continents of about 90°. This spectacular change might have caused dramatic climate changes that might have stimulated evolutionary eruptions (Kirschvink, Ripperdan, and Evans 1997).

The beginning of the Cambrian is also marked by dramatic changes in isotopic ratios in sedimentary rocks. ^{13}C enrichments may signify burial of carbon in sediments and increase of oxygen in the ocean and atmosphere (Knoll et al. 1986).

So there is no shortage of environmental change with which to associate an explosion of animal life just before or in Early Cambrian times. We cannot, however, provide a scenario that truly establishes causality. There is no smoking gun, if only because we are not yet sure where to locate the time and scene of the crime.

Innovations. Although intrinsic explanations need not be proposed to the exclusion of environmental stimuli, they depend nevertheless on the fixation in some lineage of a genetic, physiological, or morphological change that is necessary for the radiation of the animal phyla. An environmental connection becomes obvious in cases in which some environmental change is required before a morphological or physiological innovation can produce a functioning animal. Such intrinsic explanations include:

1. *Aerobic metabolism, calcium carbonate, and body size:* Evidence on the oxygen content of the atmosphere suggests an increase approximately 600 million years ago. It is possible that before this time, severe physiological limitations prevented the survival or activity of large active animals. Rhoads and Morse (1971) pointed out that current dysaerobic basins tend to lack animals with robust calcareous skeletons. Calcification, inhibited under conditions of low dissolved oxygen concentrations, might have also been repressed. Thus, the world before the Late Proterozoic might have been one that prevented large-bodied, skeletonized animals from existing. As mentioned above, the evidence from bioturbation suggests strongly that the Cambrian Explosion is not likely just a mineralization event, but it might very well be an event that combined an increase in body size and mineralization. In effect, the increase in atmospheric oxygen, occurring first around 600 million years and then again near the base of the Cambrian (Knoll 1994), might have crossed a threshold that permitted active, large, and often calcified animals.

Unfortunately, current evidence on anaerobiosis does not shed light on this hypothesis. Mangum (1991) argued that many of the current cases known of life under dysaerobic or even temporary anaerobic conditions do not apply to a Cambrian scenario, because the modern mechanisms appeared to be phylogenetically derived modifications of aerobic mechanisms. Thus, aerobic metabolism is ancestral, relative to the low-oxygen lifestyles now known.

It is not easy to disentangle skeletons from large body size. Most importantly, skeletons are support structures, especially as external skeletons in arthropods and as internal skeletons in echinoderms and vertebrates. Also, mineralized structures can be employed for functions other than skeletons, as in the teeth of some chitons (Lowenstam 1981). Although calcified tubes might protect against predators, tubes also allow a polychaete to live in a permanent home that it can ventilate and use as a settling point for detrital food or even perhaps as a microbial garden. Most of these lifestyles are associated with large body size, which might have been the significant change just before or at the beginning of the Cambrian.

2. *Developmental genes:* One of the great advances since the mid-1980s was the discovery of a lingua franca for body patterning that transcends the details of development within individual animal phyla (Akam 1987; Carroll 1996; DeRobertis and Sasai 1996). The so-called *Hox* cluster of genes contains information required for anteroposterior developmental determination. The universality of this information has been thought to be a lynchpin for animal development (Slack and Holland 1993). These rules unite the protostomes and deuterostomes (DeRobertis and Sasai 1996) and apparently represent an increase of complexity over cnidarians, which presumably occupy a more ancestral position in animal phylogeny (Martinez et al. 1998).

   The evolution of the protostome–deuterostome *Hox* cluster has been suggested to be the innovation that permitted the later Proterozoic–Cambrian radiation of the animals (Valentine et al. 1996). The latest common ancestor of the protostomes and deuterostomes had six *Hox* clusters, and episodes of gene duplication occurred in deuterostome history. It is not clear, however, that increase in number of *Hox* genes is necessary to increase morphological complexity (Warren, Nagy, Selegue, Gates, and Carroll 1994). Moreover, the *Hox* cluster is just a small part of an upstream–downstream cluster of genetically determined interactions that specify morphology. It is likely that many important parts of development lie outside the *Hox* cluster, which acts more as a set of organizers. It also may be true that natural selection for anteroposterior differentiation (which allows directed sensory perception and locomotion) facilitated the appearance of the *Hox* cluster, and not the reverse.

   The molecular data suggests a deep origin for the protostome–deuterostome split. Although a consensus has emerged about the deep Precambrian aspect of this split, one should still reserve judgment about the result, owing to the difficulties in using extrapolation to estimate the time of divergence. Nevertheless, if we accept these results, then the appearance of the sixfold *Hox* cluster could have little to do with the Cambrian Explosion, because it predated it by some 400 million to 600 million years.

3. *Nervous system:* I will use this example as a proxy for a number of other such hypotheses, such as the rise of a muscular system or a complete gut. The development of a fully developed nervous system with ganglia to aid vision and other functions, combined with the presence of a brain to integrate sensory signals, might have been the innovation required to allow the radiation of the bilaterian

triploblasts. Although this hypothesis (Stanley 1992) is attractive, it comes squarely against the molecular data discussed above, which suggests that animals capable of a fully developed nervous system might have been present many hundreds of millions of years before the start of the Cambrian.

4. *Predation or other biotic interactions:* In the Lower Cambrian, we already see a plethora of animal groups with a wide variety of ecological roles. Most noticeable are the large roving predators, including the widespread and seemingly ferocious *Anomalocaris,* which reached lengths of over a meter (Conway Morris and Robison 1988). Although some predators can overwhelm all potential prey, it has long been appreciated that a number of refuges permit predators to escape the attention of prey, especially by nocturnal habits or crypsis. But escape in size is also an effective deterrent against predation, and many invertebrate species can avoid being eaten by virtue of their unmanageable size (Levinton 1995). Thus, a simple Cambrian scenario can be developed where the rise of predation causes rapid natural selection for increased body size. This would presumably happen in many lineages and result in the evolution of increased predator body size, thus promoting an arms race. In space-limiting hard-bottom environments, predation tends to eliminate competitive dominants (Paine 1966) and maintains diversity. It might be that the rise of predation in the Cambrian performed a similar role of promoting diverse biotas of prey (Stanley 1976).

   I do not know of a study that attempts to estimate secular changes through the Cambrian in the degree of predation, as measured perhaps by shell repair damage or wounds in trilobite carapaces. It is not unusual to find pieces of trilobite carapaces missing, which might reflect predation attempts. Possibly, other biotic interactions such as competition might also have contributed to increased body size, because larger body size may permit exploitation of larger food items.

   Because we do not have an effective accounting of changes in predation through the Cambrian or of the very rise of predation itself in the Cambrian, this hypothesis is untested. Parker (1998) has found evidence for a diffraction grating on external surfaces of several Burgess Shale fossils, which suggests an adaptation to reflect color. This may be related to the rise of predation, but it could just as easily be a sexual recognition signal.

   It is very possible that predation might have predated the Cambrian, but we do not have the tools to detect it. The late Precambrian fossil *Cloudina* is the earliest animal known to have produced skeletal remains, in the form of tubes. Bengtson and Zhao (1992) found nearly 3% of tubes from the Shansi province, China, containing rounded holes 40 to 400 micrometers in diameter. A positive correlation between the size of the holes and the width of the bored tubes suggests that the attacking organism was a predator, selecting its prey for size. If true, this would be the oldest case of predation in the fossil record and would support the hypothesis that selection pressures from predation could have been a significant factor in the evolution of animal skeletons around the Precambrian–Cambrian boundary. On the other hand, we may yet find much older tubes with predation holes.

   Thomas and Reif (1993) established a scheme of skeletal structures that encompass all skeletonized organisms. As mentioned in chapter 5, such a scheme allows a calculation of the extent of morphospace that is occupied at various points of geological time. Thomas, Shearman, and Stewart (2000) performed such an analysis for Burgess Shale–style faunas and found that the bulk of skeletal morphospace was occupied by Cambrian times. Of 182 possible skeletal element pairs, 146 could be found in the Middle Cambrian. Unfortunately, this evolutionary exuberance cannot be used to test the predation hypothesis or other skeleton-related hypotheses. The dominance of single-element rods and metameric exoskeletons is strongly linked to the rise of the sponges and arthropods, respectively. A future phylogenetic analysis of these data may prove illuminating in establishing patterns of taxon-specific and polyphyletic flourishings of specific skeletal designs.

5. *Cropping and bioturbation:* The Ediacaran world appears to be dominated by shallow-water sediments capped by a biomat, perhaps algal. Up to the very top of the Vendian column, we see little evidence of the sort of bioturbation that would vertically disrupt the sediment more than a few millimeters. Then suddenly – by geological standards – the diversity of burrowers and extent of vertical bioturbation increases dramatically. So a chicken-and-egg problem arises immediately. Did the rise of infaunal bioturbators cause the widespread destruction of algal mats, allowing a plethora of new lifestyles and morphologies to arise in the Early Cambrian? Or, alternatively, did the rise of surface-grazing microbial-algal consumers cause the sudden disruption of the mats, allowing bioturbators to penetrate an otherwise impenetrable mat? I can see no evidence at present to allow us to distinguish between the two alternatives. Worse than that, it may be that some more general factor stimulated or permitted the increase of body size at the end of the Precambrian, which would allow the evolution of mat grazers and mat-disrupting burrowers. The Cambrian fossil record does not help us terribly much because the mats and Ediacaran-like preservation disappears, at least in frequency, well before the appearance of the great Early Cambrian diversity in the Tommotian and Atdabanian.
6. *Phytoplankton–zooplankton diversification and vertical transport:* This hypothesis would argue that a sudden change in phytoplankton diversity might have stimulated the diversification of zooplankton. The increase in phytoplankton, registered by an increase in acritarch diversity, might have provided an increased diversity of food supply to suspension feeding benthos, which in turn might stimulate the diversification of other trophic levels. In addition, a diversification of zooplankton, as of yet unregistered in fossils, might accelerate the rain of phytoplankton, via fecal pellets, to the bottom, thus stimulating the evolution of benthos. Although the former hypothesis is a possibility, the latter seems unlikely. Collisions between phytoplankton cells often cause the rapid origin of marine snow, which may sink rapidly to the bottom, even in the deep sea (Christensen and Kanneworf 1986; Riemann 1989; Thiel et al. 1988).

At present, we have no reason to select any one of these as necessary stimuli to the sudden appearance of a diverse animal fauna in the Early Cambrian. Indeed, our problem is that we have too many hypotheses chasing too few data.

The Main Points

1. Most of the preservable and many soft-bodied crown-group animal phyla appear in the second two stages of the Cambrian. These appearances constitute the "Cambrian Explosion."
2. The Cambrian Explosion might record an evolutionary event, the divergence of the animal phyla, or it might instead merely record an explosion of fossils. Cloud (1968) argued that it was an evolutionary event.

3. Some have argued that the Cambrian Explosion was an evolutionary event, but it might have included a period of several tens of millions of years during the Vendian, when a number of animal groups existed, some perhaps being bilaterian triploblasts.
4. Molecular clock evidence from several studies places the timing of the protostome–deuterostome split much before the Cambrian, with a concentration of dates around 800 million to 1,000 million years ago. This suggests either that the rise of animals is in deep Precambrian time or that some artifact is giving a false molecular timing signal.
5. Molecular developmental evidence suggests that the common ancestor of the protostomes and deuterostomes had a wide variety of features that could specify an animal surprisingly modern in aspect.
6. The Cambrian Explosion was not just an explosion of skeletal types but also an explosion of large-bodied animals, including those with hydraulic skeletons capable of extensive bioturbation.
7. The stimulus for a Cambrian Explosion may lie in an increase of atmospheric oxygen, but changes in climate or even crustal deformation and nutrient input from vulcanism may be implicated.
8. Intrinsic biological factors, such as the rise of *Hox* genes and the rise of a nervous system, are discountable. However, the rise of predation might have stimulated both the sudden increase of body size and the rise to dominance of skeletonized taxa.

CHAPTER 9

Coda: Ten Theses

In Thurber's fairy tale *Many Moons*, the king summons his advisors to fetch the moon for the princess. To the king's dismay, each advisor claims that the moon is made of a different substance and thinks it to be a different distance away. The court jester finds the solution. Obviously, each advisor sees the moon differently. Just ask the princess what *she* thinks. Only then will the king know what to do. As it turns out, she thinks the moon is smaller than her fingernail and is made of gold.

Evolutionary biology suffers from much the same diversity of viewpoints and expectations. We tend to forget the importance of other perspectives and areas of study. Schindewolf saw evolutionary change through the perspective of the fossil record. Just like the princess looking at the moon alongside her fingernail, one is likely to draw incorrect conclusions. In more recent years, paleontological studies have injected a number of exciting and substantive ideas into evolutionary theory, even if the fingernail perspective is sometimes apparent. By ignoring the dimension of geological time, population biologists heretofore have largely ignored the colossal biotic changes that have swept the planet. Molecular evolutionists and students of molecular adaptation have ascended to prominence, and sometimes it seems as if they feel that a complete catalogue of genes and nucleotide sequences will solve the deep problems of evolutionary biology. But to dismiss the new knowledge of the genome as mindless reductionism is to miss the most important window we have on organismal organization. It's just that the window is still very dirty.

The great panoply of evolutionary scales and perspectives *have* brought us a number of generalizations and perhaps a greater number of paradoxes and questions. I hope that a brief summing up will provide some tracks to guide future evolutionary lines of thought. Like the frontispiece, my thoughts will not clickety clack down a straightline track; they will come together and come apart.

I. The Stabilization of Form

The history of life has witnessed a stabilization of form along a number of tracks, consisting of the evolution of more and more discrete body plans, following bursts of evolutionary radiation. On the other hand, there is no particular evidence that has emerged that justifies the notion that form diversity has declined after an early shakeout at the base of the Cambrian.

It is not clear how long it took for the metazoa to arise, but a large number of crown-group phyla appeared as fossils in a brief time span some time near the beginning of the Cambrian. Most of the extant animal phyla appeared early in the Phanerozoic and the bulk of taxonomic turnover occurred subsequently at lower taxonomic levels. I believe that this is the single most important fact that the fossil record has contributed to evolutionary biology. Indeed, in the Permian extinction, the large majority of the species became extinct, but no new phyla arose after a seeming wide opening of ecospace. The void was refilled with most of the same old characters in slightly new developmental and morphological guises. The notion that phyla appeared first is not just an artifact of taxonomy's correlation with time of origin. A series of body plans took hold on the earth and subsequent evolution has been a play on these basic themes.

Why haven't lineages bearing these basic body plans "broken out" of the mold and given rise to new phyla? I believe that the general model of an evolutionary ratchet (chapter 4) is the key. Functional, developmental, and genetic ratchets have combined to ascribe a high burden, *sensu* Riedl (1978), to any prospective change. There has been no drift from a set of basic body plans sufficient to preclude their identification in overall developmental plan with the phyla that became established in the early Paleozoic. At lower taxonomic levels, however, long-term stability is also apparent. Many body plans and styles of living have remained essentially unchanged for tens to hundreds of millions of years, despite extensive speciation, the rise of many new groups, and significant changes in environmental conditions. The centripetal force of habitat selection must also matter.

It is therefore our task to understand the contribution of the three ratchets to the stabilization of the number of phyla and of morphology. If, for example, developmental or genetic constraints are most important in evolutionary conservatism, then there is some justification for taking the phyla to be baupläne, much as the essentialists, such as Cuvier and Owen, defined them. But we would have a mechanistic explanation for invariance. Variations within the phyla would be minor variations on a theme constrained by developmental and genetic (that is, internal) controls that prevent significant evolutionary change. But if functional considerations, particularly strong functional interactions among body parts, are the major source of stabilization, then the presence of a few body plans may simply reflect the survival of those that work. The description in chapter 4 of the evolution of developmental programs suggests that functional, developmental, and genetic constraints evolve in concert, leading to complex phenotypic interactions. It is inappropriate to divide such patterns into adaptive and nonadaptive components. Indeed, the so-called internal organization has a functional aspect to itself, as it necessary for functional reasons for developmental plans to evolve that elaborate a series of developmental "objectives," including body axes, timing of appearance of gene expression and other developmental phenomena. I argued in chapter 4 that the overall stabilization of form has not been caused by a freezing of developmental programs. Indeed, the evidence leads to a far different conclusion.

The assembly of a *bauplan* may involve many, or just a few, steps. We might argue that in some cases singular novelties led to a fundamental reordering of evolutionary directions. If "mammalness" can be defined only with a fairly large number of strongly interactive characters, "molluskness" may have been defined by the two innovations of spiral deformation during development and a cap-shaped shell.

This subject is difficult to approach constructively, as it is easy to fall into the trap of subconsciously reifying a set of phylum-level traits into an essence that we believe to resist change simply because we know that the traits have survived. When we unite the arthropods by a flexible cuticular exoskeleton, we imply that the cuticle appeared early and remained stable for most of the taxon's history, without proving that the cuticle was retained because of its functional, genetic, or epigenetic burden. The same can be said for the larger phylum group Ecdysozoa. Descriptions of time course must, therefore, be accompanied by testable hypotheses on the trait's burden. Ernst Haeckel took the "tadpole" stage of development to be a fundamental indication of common ancestry of the classes of vertebrates that had never been altered in evolution. In more modern parlance one might hypothesize the tadpole to be an epigenetically constrained stage. But earlier, and later, developmental stages of vertebrates are taxonomically more diverse, as Haeckel's own work demonstrated. Thus the tadpole can be interpreted as a form retained by some functional consideration.

Despite this danger, it does seem clear that the time course of commitment seems to involve early acquisition of traits, with subsequent stability. Presumably, the stability represents the achievement of functional integration, which would have a high level of fitness loss if it were changed significantly. The morphology and even detailed behavior (as indicated by fossil morphology and preservation) of many groups have changed little since their appearance.

I see this evolution of stabilization as a process of commitment, which occurs on developmental, functionally integrational, and ecological levels. It is a trap in a way, but the trap involves increases of fitness. Relative to antecedents, such increasingly stabilized forms must represent true progressive evolutionary events. That is to say, later developmental cycles beget fitter individuals than developmental cycles earlier in the group's history. If this means that I am admitting to a belief in evolutionary progress, then so be it, as long as you are clear that this is within an evolutionary and ecological context of ancestors and descendants playing about the same ecological role. It makes no sense to speak of later forms being superior to any but their antecedents. It also is likely that the evolution of stabilization reaches a peak very early on. It therefore may be that a Jurassic, or a living, crustacean has absolutely no greater fitness in terms of developmental integration and ecological function than its predecessors in the Early Cambrian.

II. No Evidence for the Sudden and Nearly Simultaneous Rise of Basic Body Plans

Here is the paradox. While there is evidence for the evolution of stabilization (e.g., more specialization of taxa over time in an evolutionary radiation, stabilization of developmental programs to the degree that they do not change much), there is no real evidence that a series of baupläne sprung up in the form of an evolutionary lawn. Indeed, as the evidence in chapter 8 attests, the more we look, the more tree-like phylogenetic structure we find among and within the animal phyla. A formerly bizarre and disparate 21 classes of echinoderms has been rendered into a typical tree. Indeed, many groups of phyla no longer seem to be so distinct in morphology, distant, or polyphyletic in taxonomic structure. The most spectacular change of perspective comes from the great Cambrian radiation itself. Harry Whittington and colleagues, as discussed in chapter 8, were taken with, and eventually overcome by, the bewildering forms in the Cambrian. This led to a hardening of the evolutionary lawn hypothesis. But subsequent research has demonstrated that the apparent great sudden diversification of form in the Early and Middle Cambrian was mostly an illusion. Once the cracks were filled a series of fascinating, but essentially tree-like relationships emerged. The lawn was supplanted by the ever-dividing branches of a forest tree. We get the impression that early representatives of many groups gave an impression of ancestral fuzziness, relative to the characters of what we often call crown animal groups, which appear a bit later in the fossil record (often by the Ordovician). The newest evidence using molecular clocks suggests a possible long Precambrian interval of divergence of the animal groups.

The Hox genes and their widespread occurrence do not displace this conclusion. While it is true that Hox genes have a fundamental and widespread role in determining body axes, we have absolutely no evidence that any revolutions in the deployment of these Hox genes led to a sudden flowering of body plans of necessarily disparate form and ecological function, corresponding to the crown phyla. Indeed, the Hox genes are classic characters that unite all of the animal taxa by means of symplesiomorphies, or shared ancestral characters; they do not define a set of shared derived traits (synapomorphies) corresponding to the body plans. If there are other sets of Hox gene-like characters that uniquely identify a set of body plans we have yet to find them. Instead, we find that the Hox genes were deployed throughout development for different developmental functions, being used much like a limited set of tools in a toolkit.

The thesis that body plans arose at first by splitting and successive subdivision of an original evolutionary line is fundamentally at odds with the first thesis of continual stabilization of a diversity body forms over geological time. How can we be sure, or even define criteria to tell us that the many separate lines have evolved their own increasingly stabilized developmental programs? I am afraid that our evidence is mainly emotive. When the great mass extinctions occurred, as at the end of the Permian, no new phyla appeared. This statement has strength when one realizes that the living preservable phyla were more or less all identified before we really knew their occurrence over geological time all that well. This means that we have long recognized phyla by something other than their cladistic structure. The criteria involve a series of syndromes of distinct morphologies and developmental plans. No one regards the splits between mollusks, arthropods, nematodes and the like as strange, even though we have reckoned more recently a larger phylogenetic structure (protostomes [ecdysozoa, lophotrochozoa], deuterstomes).

III. Fundamental Aspects of the Evolution of Development Are Plastic

Even though overall form has proved to be remarkably stable, there is no compelling evidence that evolutionary programs are rigid and unassailable by evolutionary change. Indeed, it is clear that the most fundamental aspects of developmental programs such as gastrulation and order of cellular division cycles can be changed completely, with no great change of overall form. Seemingly trivial ecological selection forces, such as those that change egg size, can completely reorganize early development, yet the organism grows up to be something much like its ancestors have always been. Despite a complete reorganization of early development, the genus *Gastrotheca* has individuals that grow up to be an ordinary frog. So it goes in many other cases, as we have described in chapter 4. We are only beginning to appreciate this variation, because in the past developmental biologists have been far too attentive of the great constancies in development but have ignored the variation. This continues to be true in recent years, when universal laws of Hox genes have forestalled our discovery of the truth that fundamental developmental genetic mechanisms, ranging from those controlling gastrulation to sex determination, can disappear with surprising ease in an evolutionary lineage. It appears that when all is said and done, it is the form and function of the organism that is constant. If we push that swinging door open and look into the kitchen of development we find that new needs are often being satisfied by radical new uses of the pots and pans that can be reorganized and shuffled to cook, yet the same dish emerges from the kitchen to look and taste the same.

IV. Adaptive Evolution Has Centrifugal and Centripetal Components

Given sufficient genetic variation, a change in the environment can cause a rapid and extensive response via natural selection. This is the centrifugal component of evolution, which permits adaptation to new environments. What is amazing is the boundless variety of genetic variation in living species. Nearly any morphological trait that has ever been examined has allelic variation. As shown by both living and fossil examples, gradual change is rampant and the responses in living populations are expected to be very rapid. Indeed, bouts of natural selection are probably intense and short. This is the lesson taught to us by combining the nature of function, which has many local stable optima and genetic variation, which can be exhausted for a time. There is a limit to the centrifugal component since population variation is often insufficient to make an adaptive (and morphological) leap. It is misleading to emphasize only the large number of characters that are very heritable when considered individually. By doing this, one overlooks the difficulty of finding combinations of variants in complexes of characters that likely prevent the evolution of a population from one morphological mode to another that might increase fitness.

An underemphasized centripetal component in evolution slows down the rate of evolutionary change, sometimes even in the face of environmental change. We have discussed in chapter 4 the obvious genetical and developmental constraints that might create such a centripetal force, but there are also important forces that relate to functional interactions.

Functional constraint has several components, including (a) habitat choice, (b) functional interaction of traits, and (c) harmony of traits with the environment. Habitat choice is a major component in the stabilization of the phenotype, as it traps the organism in the same milieu. Larval selectivity of marine invertebrates assures that a dispersal stage will "find" the parental habitat. This keeps the animal in a similar substratum for many generations, but also assures that an organism well adapted to muds will not stray into sands. In cases where larvae will surely be swept to inappropriate areas, adaptations for larval retention exist, as in estuaries (Levinton 1995). It is a telling point that Pleistocene migrations of latitudinal climatic belts have usually been accompanied by latitudinal shifts of vegetational zones, but not in a major evolutionary change in the degree of temperature tolerance sufficient to permit a species to stay put and survive the onslaught of climatic change during a glacial advance. The enslavement of organisms to their shifting environments is the essence of the fossil record, which records the shifting of sedimentary facies and their associated fossils. It is the basis of Walther's Law – one of the most fundamental precepts of stratigraphy – that sequences of environments (and associated fossils) will be identical both laterally and vertically. This can only be true if fidelity to a home environment (facies) supersedes the effects of strong directional selection to jump to a new adaptive mode.

An important component of stasis must be the relatively high cost in fitness of making the leap to a new mode. Although there is a degree of plasticity, most organisms tightly bound to a substratum are integrated in form and behavior such that they do best in one sediment type. Thus, natural selection cannot act efficiently to effect a habitat shift, because all organisms are destroyed. Thus stasis by habitat choice can only be effective if mistakes are largely fatal. An important evolutionary theorem is that directional adaptive evolution in a novel habitat type will not occur if the initial drop in fitness concomitant with a habitat change is too great to compensate for the slow incremental increases in fitness conferred by adaptations that secure increased ability to find the organism's current preferred habitat.

Though modes of tissue interaction and the order of appearance of structures in development may well be fixed by genetic and developmental constraints, it seems unlikely that most of the fixed arrangements of external morphological traits found in long-lived fossils can be explained in this way. Most of the constancy we observe falls in morphological traits that are known to be heritable, and major changes can be effected in laboratory populations under favorable conditions in a few generations. This is even true of strongly canalized traits (e.g., Rendel 1959). But the movement of a founder population to a new and qualitatively different habitat constitutes the strongest directional selection we can imagine. The lack of evolutionary potential, however, is clear when one considers the very low probability of the appearance of a mutant that is suitable to the new environment. Its low frequency would diminish its probability of fixation, as its colonizing population would have an extremely low probability of lasting more than one generation.

Catastrophic directional selection is therefore likely to be usually ineffectual. This would suggest that most Wrightian landscapes effectively have only one peak: The one that the population now occupies. Stabilizing selection therefore is the predominant mode throughout biotic history.

Stabilizing selection remains as evolution's most mysterious process. On the one hand the evolution of phenotypic response can be visualized as a competition between the evolution of plasticity and canalization. The first property serves the organism well when an unpredictable environment reduces the fitness of genotypes with a fixed response. Canalization, on the other hand, ensures that an optimum phenotype will be expressed despite environmental variation. Canalization may involve a phenotype's indifference to environmental perturbations, but it also may involve the evolution of stabilization of the phenotype, despite some considerable variation in genotype. We still cannot readily predict whether phenotypic plasticity or canalization should dominate phenotypic determination, but these factors are probably behind why we have varying patterns of evolutionary change.

V. The Fossil Record Is Readily Extrapolated from Population Variation, Genetic Determination, and Natural Selection; No Higher-Level Evolutionary Process Is Required

The closer we look, the more gradual the fossil record turns out to be. This conclusion is only stronger than when I first asserted it in the first edition of this book. While the modes of character determination are still difficult to understand in many fossil populations, there is still no reason to doubt that within-population processes explain the evolutionary change we observe in the fossil record. Of course there would not be lions and wolves, dandelions and palms without speciation. The essence of divergent evolution is the establishment of a series of reproductively independent evolutionary units. But speciation itself still does appear to be necessary to *beget* the amount of evolutionary change necessary in evolution.

Haldane presented his paradox in 1949: evolution appeared to be so slow as to be determined by genetic drift. But we now know that the paradox is completely resolved when we examine the time scale over which evolutionary divergences have been measured in the past. They simply average out the strong turbulence of shorter-term evolutionary change, which occurs at much greater rates. Longer periods of geological time tend to include more periods of nondeposition and periods of stasis or reversals in the pattern of evolution. These longer periods are those which have given us our general impression of very slow rates of evolution. Owing to this bias, we know little or nothing about absolute rates of evolution from the fossil record. Long-term stasis (i.e., a lack of a trend) may still prevail, despite a spectrum of rates.

Sustained long-term directional change in single characters is unlikely on functional grounds and new rearrangements of complex characters are required to effect major evolutionary change, which often awaits unusual mixes of characters or the appearance of wholly new environments.

I continue to be surprised at the warm reception of the argument that there are so many unexplained and peculiar organisms that we must conclude that natural selection for increased fitness is not the main driving force of evolution. The Spandrels of San Marco metaphor leads us to believe that we must choose between a pervasive form of expectation of optimality, much like a set of an engineer's ground-up designs, as opposed to accepting the panoply of organisms, replete with peculiarities of different bumps and spines. I see this argument as completely bogus. Evolutionary biologists understand that the hand that is dealt to an evolutionary line must surely influence its adaptive evolution. Natural selection is contextual and optimality should only be viewed in the context of available materials, as I discussed in chapter 5. Given that mutation is not unlimited and organisms often have a complex history, it is no surprise that small and sometimes peculiar differences are seized upon by natural selection, leading to a complex series of evolutionary trajectories. Combined with extinction, this has led to the weird and wonderful assortment of living groups that have populated the earth. But it is virtually silly to believe that the very existence of this diversity falsifies the dominance of natural selection in the shaping of evolution.

Punctuated equilibrium ascribes a special importance to speciation as a major cause of morphological evolution. The remaining history of a species is regarded as a quiescent period, as the species has a homeostatic mechanism that resists change. Trends in evolution are therefore variations in speciation and extinction rates, and phyletic evolution is therefore an incomplete explanation of evolutionary trends. Gould (1985a) sees the theory of punctuated equilibrium as the cornerstone of a larger hierarchical theory of evolution, though Sober (1985) shows that punctuated equilibrium is not a necessary prerequisite for such a theory.

My discussions in chapters 3 and 6 suggest that the theory is not viable. There is no evidence that phenotypic evolution is necessarily, or even commonly, causally associated with speciation. Allozymes, chromosomes, DNA sequences, and morphological evolution all fail to show a significant break at the species level. Speciation is caused by a variety of genetic processes that lead to intersterility. When the establishment of sterility coincides with adaptive evolution, one can indirectly associate speciation with phenotypic evolution. In these cases, however, speciation is the effect of phenotypic evolution or it is merely coincidental with phenotypic divergence.

Critics of the punctuated equilibrium theory are blamed for misunderstanding its import, which is the significance of stasis in understanding the evolutionary process. Stasis is an important characteristic of many lineages. But this does not necessarily prove the importance of speciation in breaking stasis, nor does it explain constancy of species properties because of membership in a single species. After all, many genera and families are remarkably phenotypically homogeneous (e.g., Wake et al. 1983). Rampant speciation seems not to beget phenotypic diversity in a wide variety of groups that comprise sibling species complexes. Surely one cannot credibly assert that a morphology such as that of *Lingula* has not changed much for lack of speciation. We know that shell characters can change dramatically within local populations, let alone over hundreds of millions of years. Stasis is interesting, but there is simply no body of evidence that relegates its cause to a failure of speciation.

Fossil data can be used to ask whether phyletic evolution is sufficient to permit extensive morphological divergence. The bulk of the evidence suggests that speciation is not required for major morphological evolution, and certainly not at the level denoting typical species differences. Unfortunately, this is not an adequate test of the punctuated equilibrium hypothesis, which asserts the predominance of speciation as a cause of morphological evolution. The evidence, however, does show that phyletic change is common and sufficient to generate large-scale evolutionary change (chapter 6).

The research emphasis started by Eldredge and Gould (1972) has had a positive effect in stimulating a number of studies of transitional evolution. But most of the debate has proceeded with examinations of character change with no genetic mechanisms in mind. As a result, traits that might be strongly or weakly canalized have all been blended together and subjected to the litmus test of stasis versus gradual evolution. This approach is naive and makes most of the arguments in the literature rather sterile. The same problem holds for the question of discontinuous versus continuous traits. We cannot hope to understand the many patterns found in paleontological data without some models of genetic determination in mind. After all, a meristic trait such as bristle number can be strongly canalized or can be quite labile and subject to rapid directional selection. Similarly, strong phenotypic shifts in shell form can be quite difficult to accomplish, or may be under the control of a simple genetic polymorphism (e.g., Palmer 1985). This ignorance leads to futile debate. Pattern does not map uniquely to process in the question of stasis or varying rates of evolution.

The punctuated equilibrium hypothesis would harken us back to the essentialism that we escaped in the neo-Darwinian period mentioned in chapter 1. At this time, Fisher, Haldane, and Wright combined Darwin's theory with the algebra of genetics and formulated a way of looking at evolutionary change that has had an astounding degree of success. The founders of the Modern Synthesis carried this information into the practice of systematics and natural history, and found it to be an essential tool in the understanding of the evolutionary process. The empirical discoveries of the past forty years would not be very useful without this theoretical groundwork. Indeed, the force of the neutral theory of molecular evolution is its contrast with the theory and practice of preceding decades. While there still are a large number of enigmas concerning the structure of the genome and mechanisms of speciation, the population thinking founded by Darwin and carried into the twentieth century by the neo-Darwinians and the Modern Synthesis, still stands as the best framework for understanding adaptive evolution. We have tried to lay essentialism to rest; one of its descendants, the punctuated equilibrium hypothesis, deserves a similar fate.

VI. Saltation Is a Nonproblem in Evolution

The presence and explanation of morphological gaps between organisms has been a continuing theme in biology. While pre-Darwinians presumed gaps, by virtue of their typological approach to biology, a succession of debates among evolutionary biologists has revived the question of discontinuity. Indeed, a recurrent theme in evolutionary biology is why there appear to be clumpings in morphospace. The argument was important in the debate between "biometricians" and "geneticists," where the former camp thought continuous variation to be the stuff of evolution, and the latter group saw discontinuous mutations as the driving force in evolution.

The main reasons for gaps in morphospace among members of the same phylum are divergent evolution, extinction of intermediates, and functional limitations, working within the constraints of a group of constructional plans, such as the logarithmic spiral shell.

The astounding range of intermediate forms that have been discovered as fossils suggest a long history of cladogenesis, phyletic evolution, and extinction of intermediates, though rapid evolution between modes must have typically been the case. Where ancestors and apparent descendants have been found in the fossil record, subsequent collections have often filled in the gap with intermediates. Integrated phenotypes in the mammals can be shown to have congealed over time, suggesting the process of adaptation in creating the gaps via divergence. In other cases, such as in the mollusks, gaps in morphospace are not filled for functional reasons.

The mechanisms that generate variability, constrain direction, and create some saltatory effects in mutations are of great interest, but largely secondary to the three processes mentioned. This is not to say that all functionally harmonious forms have existed throughout geological history; historical accident has prevented any number of imaginable morphological constructs.

Recently, as has been true periodically thoughout the past 100 years, there has been revived emphasis on phenotypic discontinuity, with developmental mutants taken to be the evidence for the potential for saltation. This argument has ranged from the reasonable assertion that some discontinuities stem naturally from the mechanisms of genetics and development (e.g., Alberch 1980), to the unreasonable presumption that, just because developmental anomalies are present, they might be a vehicle for rapid and saltatory evolutionary change (Løvtrup 1974; Gould 1980a). We have discounted the latter in chapter 4, but the former follows from all we understand of the genetic determination of traits. Indeed, this knowledge has been left to us by some of the orthodox founders of the neo-Darwinian movement.

We err by taking present-day discrete phenotypic organization and developmental anomalies and presume that they imply saltation. This error is traditional, and mimicks Punnett's (1915) error of confusing the current genetic organization of mimetic butterflies as evidence of a saltatory origin. We now know that strong canalization among morphs, tight linkage among genes controlling the same trait, and switch genes that control batteries of other genes, are mechanisms that now control discontinuity, even if the origin of the trait's organization happened to be gradual. The vast array of studies show that even seemingly invariant traits are regulated by many genes and that the constancy has been fixed by the evolution of thresholds that enhance the canalization of the trait. This constancy must be reinforced continuously by the action of natural selection, as relaxed selection usually leads to a loss of integration of a trait (e.g., eyes in cave fishes).

While the history of many groups has not been the path that might be designed by an engineer, the role of adaptation in producing the clumpings in morphospace is quite clear. Today, after more than a decade of debate about above-species level processes, I believe that no knowledgeable scientist entertains seriously the notion that complex structures such as eyes, jaws and limbs evolved by shuffling of traits acquired by random fixation during speciation events.

The proponents of saltation in recent years have not presented a clear picture of why neo-Darwinian concepts fail to account for discontinuity, or evolution mediated by alterations in development.

Examples that are commonly cited as hopeful monsters, inconsistent with neo-Darwinism (e.g., Frazzetta 1970), typically involve variation requiring fairly trivial mutations that can easily be imagined to arise within typical populations. Surely, the developmental mechanisms that have been recently popularized were discussed (with different specifics) back in the 1920s and 1930s (e.g., Ford and Huxley 1927; Haldane 1932b). Maderson et al. (1982) argued that developmental mechanisms producing variation in form are not congenial with the Modern Synthesis. But the mechanisms they discuss are not antithetical to any questions of genetic determination of variation. Indeed, P.F.A. Maderson (written communication, 1985) admits that this is so. Gould (1984b) has revived Mivart's old challenge that many structures must have been formed by saltation, because functional intermediates (half a wing, half an eye) are inconceivable, but even here, Gould has been inconsistent, even contradictory, in his arguments. He writes:

> At the higher level of transition between major organic designs . . . gradualism has always been in trouble. Although it has stonewalled with commendable tenacity. No one has ever solved Mivart's old (1871) dilemma of "incipient stages of useful structures." (Gould 1984a, p. 14)

But, elsewhere, Gould states:

> I believe that Darwinism has, and has long had, an adequate and interesting resolution to Mivart's challenge. (Gould 1985b, p. 14)

Discontinuity in morphological evolution is surely an issue, but hardly one that shakes the foundations of neo-Darwinism.

There seems to be no real reason to abandon the conclusions of the neo-Darwinian era: Most mutations are of relatively small effect and larger-scale mutations, though known to occur, usually reduce fitness. Therefore, smaller-scale mutations probably are more important in evolution. Major saltations are not precluded so much as improbable. This is not to preclude discontinuity. Indeed, as I have mentioned, discontinuity has been a prime area for research in the area of transmission genetics. But no recent claim for discontinuity has been inconsistent with neo-Darwinism.

The interesting notion of developmental constraint (e.g., Gould 1977; Levinton 1986; Maynard Smith et al. 1985) is an important addition to the study of adaptation, but hardly at odds with Darwinian theory, nor does it require great leaps of morphological evolution (or faith).

VII. Character Evolution is Strongly Affected by Organismic Integration and Compartmentalization

Although many characters evolve rapidly and often, it is equally true that others have remarkable stability. The evidence from the fossil record, as discussed in chapter 6, suggests a range of rates of morphological evolution, including what I have termed character stasis. While it is indeed possible that factors such as genetic and developmental constraints shape the course of evolution, there is no particular evidence to falsify the notion that function is the major factor in constraining rates of evolution. Features that are strongly canalized are obviously constant as the result of a genetic-physiological mechanism. But laboratory studies (Waddington 1956; Rendel 1959) show that canalization itself is subject to alteration by selection. Strong directional selection can move the genotype – phenotype interactions into a new regime where constancy is now substituted by variability in a population. A constancy that appears to be shaped by developmental constraints may actually be an ephemeral mechanism to stabilize the phenotype, but alterable by directional selection.

There are functional bases for variation in rates of evolution among characters. The best example of this comes from the relationship of function to the rates and patterns of molecular evolution. Genes that encode proteins with highly constrained functional interactions are those that are most conservative in the evolution of amino acid sequences (e.g., histones). In contrast, genes that encode proteins whose change in function is more loosely related to amino acid sequence are those that evolve very rapidly (e.g., the fibrinopeptides). Silent nucleotide sites evolve far more rapidly than those involving amino acid changes. Because proteins interact with others, functional interactions probably cause a form of molecular coevolution to occur. We have an analogy with what we perceive to be functional restrictions and interactions in morphological evolution.

The nonadaptive component of discrete variation and long-term constancy in many traits has been misrepresented as evidence against the crucial importance of natural selection and adaptation. There is nevertheless a clear role of developmental interactions in imposing a centripetal force in evolution.

While there is a considerable plasticity in evolution, both developmental and genetic evidence suggest that the direction of evolution may be constrained by extant interactions in epigenetic and genetic pleiotropy. Current interactions in development may preclude certain pathways of evolutionary change. As shown in chapter 4, the dependence of one tissue upon another for induction could reduce the fitness of mutants that permit independence among these tissues. This is the basis for both the notion of developmentally based stasis, and the low probability that developmental mutants of strong phenotypic effect are the stuff of evolution. There may be units of the phenotype that are bound together, but relatively independent of other blocks. The question is what binds traits together, and whether this binding is sufficiently permanent that evolutionary direction is constrained.

Genetic pleiotropy may contribute to the construction of blocks. Some of the atavisms discussed in chapter 4 suggest that sets of genes may have been retained that still have the capability of switching on structures that have been long absent in a given lineage (e.g., toes on horses, limbs on whales). This may be due to epigenetic pleiotropy, or to genetic pleiotropy, which precludes loss of either the genetic or epigenetic mechanism. In the latter case, we might imagine that the genes determining the epigenetic track may have changed over evolution, but the epigenetic process itself has been maintained. This, of course, does not eliminate the role of the underlying genes in evolution. The epigenetic mechanism may be the constrained phenotype but the genes are the only means of transmitting information between the generations.

While tissue interactions are likely to channel evolution in certain directions, the integral nature of the phenotype is due to the continual action of natural selection. The maintenance of blocks by genetic or epigenetic pleiotropy has yet to be established. The continual role of selection is best seen when a structure loses its former function. Fishes living in caves show varying stages of eye reduction, relative to their close relatives in nearby sunlit streams. But as eyes are reduced, the intercorrelations among parts of the optic system lose their formerly strong phenotypic correlation. The regressive evolution has proceeded quite differently in different populations and has involved the effects of more than ten genes (Wilkens 1971). While the mammalian cranium is an integrated functional unit, genetic correlations among parts of the unit often do not fit the expected correlations expected from function (Cheverud 1982). This argues that stochastic processes often generate genetic correlations that are maladaptive, but natural selection maintains the functioning integrated phenotype. Therefore, the aspect of channeling suggested by the concept of developmental constraints cannot operate without the continual action of natural selection. Any genetically or developmentally constrained variants that are not functionally harmonious will be culled out by this process.

The question is how to quantify the degree of organismal integration, and to dissect its genetic, developmental, and functional components. To approach this problem, models have been developed that dissect total phenotypic variation into genetic and phenotypic correlations (e.g., Cheverud 1982). These correlations may be contrasted with those expected from functional models, and the deviation can be considered the degree to which the generation of among-organism variation creates functionally disharmonious morphologies. This approach can be extended to tissue interactions and the possible role of developmental constraints in preventing the evolution of functionally optimal morphologies.

VIII. We Still Do Not Understand the Beginning, or What Controls the Rate of the Beginning

A fascinating discordance has emerged from the comparison of molecular divergence studies and first appearances in the fossil record. The origin of modern groups of birds and mammals and the origin of mammals all have been estimated by molecular studies to precede the currently recognized first appearances of the groups in the fossil record. This discordance has generated much controversy. The simplest solution to the paradox is to find the fatal flaw of either method. Molecular clocks have many assumptions built in, many of which are quite troubling. Most important of all is the assumption that the rate of sequence evolution has not changed significantly. In the case of the Cambrian "explosion" it is conceivable that an acceleration of molecular evolution creates a bias that causes us to overestimate the divergence time. On the other hand a number of studies have attempted to remove this bias and still a consistent Precambrian origin crops up again and again (see chapter 8).

On the other hand, we can point the finger to an incomplete understanding of the fossil record. As discussed in chapter 8, even a misperception of where fossils *are expected to be preserved* can trap paleontologists into looking for a long time in the wrong places. Some now famous fossil localities (e.g., the Lower Cambrian of China) were known long before their significance was appreciated. Just a newly appreciated type of preservation in phosphatic rocks has led to radically new ideas of the potential for fossil preservation. The great advances in radiometric dating have also shifted our perceptions and it may be that some startling new dates will emerge for that important time that defines the animals found as fossils in the rocks beneath the Cambrian, especially in the Vendian.

Underneath it all, we may be simply looking for the wrong things. For decades, paleontologists had the habit of finding strange fossils and assigning them to new taxa of very high rank. Thus we had a long period of naming new classes of Echinoderms and believing that there was far more phylogenetic branching of animal phyla than there apparently has proven to be. This reached a height in cases such as claims by the likes of Preston Cloud that the animals were likely to be polyphyletic or claims by Harry Whittington and colleagues that there was a great diversity of unrecognized phyla in the Cambrian.

The recent reanalyses have benefited greatly from the appreciation of character analysis and the mapping of characters onto trees. Equally important is the realization that we should not be looking for characters of the modern crown groups in the early branchings of the evolutionary tree. Rather we should be searching for organisms that are far more ancestral. Nevertheless, these organisms may reveal character complexes that demonstrate that the molecular dates are in fact correct, and that the crown groups had antecedent with their own unique character complexes that will soon be recognized. Given the surprises of the 1990s, I would not dismiss the possibility of many discoveries of so-called modern mammal ancestral groups before the Tertiary and, I hope, a similar menagerie of distinct Precambrian antecendents of the modern animal phyla.

IX. The Hierarchical Structure of Life Eludes Us as A Successful Framework within Which to Discover Evolutionary Change and Success

As mentioned in chapter 1, the analysis of life lends itself to thinking in a hierarchical context. So has this helped us very much in understanding the evolutionary process? In a sense this is the major challenge that Antoni Hoffman posed in his book *Arguments on Evolution*. Hoffman was a skeptic about the contribution of an understanding of higher levels of organization of the biosphere to the evolutionary process. I differ from this opinion, but only in a limited way. If higher-level organization matters, it appears in the main to work from the top toward the bottom. That is why extinction, especially mass extinction was such an important shaping force in the history of life. The elimination of entire groups opened up ecospace for the invasive evolution of new and often unrelated groups. Such endings were sudden in comparison to the broad sweep of geological time. On the other hand, there seems to be no doubt that the main creative force in evolution has been the appearance and fixation of new mutations. It is true that evolutionary radiations have proliferated these fixations. But overall, I am impressed with the transcendence of the Darwinian "long argument."

X. The Unexpected Will Overwhelm Our Preconceived Notions

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Glossary of Macroevolution

Relevant chapters are noted in brackets.

accelerating differentiation Increasing geographic differentiation over many loci, following isolation established by differences at only a few loci. [3]

adaptation A historical process in which natural selection leads to an increase in performance of an organism. Performance is judged against a model of optimality, given a series of boundary conditions of evolutionary history and environmental constraints. [3]

adaptedness A static description of the current functional superiority of one phenotype (genotype) over another. [3]

adaptive landscape A model describing a series of fitness peaks and valleys, as a function of genotype. The highest peak connotes the genotype with the highest fitness, though small peaks may be present. [3]

allometry The relationship between change in shape and overall size. [5]

allopatric When two populations or species are isolated from each other. [3]

allopatric speciation The origin of two or more species by means of one or more physical (geographic) separations. [3]

allozyme An enzyme that is one of a series of alternative gene products of a given locus. [3]

anagenesis *See* **Phyletic evolution.** [6]

analogy The possession of a similar character state by two taxa, on the same location of the body, but owing to a factor other than common evolutionary origin of the taxa. [2]

atavism A reappearance in an organism of a trait that had been long lost in its ancestors. [4]

background extinction The average extinction rate during a period of geological time, excluding times of extraordinary and sudden high extinction. [7]

balance school School of population genetics that argued for the importance of maintenance of polymorphism chiefly by heterozygote advantage. [3]

biological species concept View of species as a series of groups that are reproductively isolated. [3]

Burgess Shale A formation confined to a small area in British Columbia, Canada, but Burgess Shale–like fossils consisting of organic films can be found in Lower and Middle Cambrian rocks throughout the world. [8]

Cambrian Explosion The appearance of a wide range of triploblastic phyla and other higher-level taxa in the Lower Cambrian or perhaps a few million years before. [8]

canalization The case in which the same phenotype is expressed, despite some variation in the genotype. The more constancy of expression, the stronger the degree of canalization. [4]

character stasis Long-term constancy in a phenotypic character within a lineage. [6]

clade A group of species that have descended from the same species. [2]

cladistics The study of genealogy, principally using the method of grouping taxa by their shared derived character states (synapomorphies). [2]

cladogram A diagram, in the form of a tree, grouping taxa by their synapomorphies. [2]

classical school A school of population genetics that argued for the importance of directional selection and, by extension, the likelihood of reduced polymorphism in natural populations. [3]

cline A monotonic geographic change in average phenotype or genotype in species. [3]

coding regions Those parts of the DNA used in the transcription process that leads to production of a protein. [3]

codon A triplet nucleotide sequence that codes for a specific amino acid or for termination of transcription. [3]

cohort loss curve Change in number of taxa, forward or backward in time, relative to the ones present at a reference time datum. [7]

compartments Developmentally integrated group of cells whose fates are very closely integrated by cell–cell interactions and relatively independent (at least at any one time) of other compartments. [4]

concerted evolution The presence of families of identical genes. [3]

constraint non-random channeling of evolutionary direction. [4]

constructional morphology The field of morphology that argues that an organism's morphology can be explained as a combination of phylogenetic history, functional considerations, and boundary conditions imposed by the architecture, chemistry, and so on, of the organism. [5]

conversion *See* **Gene conversion.**

coordinated stasis Hypothesis that fossil communities often consist of a group of species that coexist with little extinction for millions of years, punctuated by a sudden turnover of species. [7]

correlated progression A hypothesis of multicharacter evolution that argues that character complexes evolve as an interacting process, whereby some evolutionary changes in the phenotype cannot be made until others occur. [6]

crown group A taxon that is attached to a cladogram in a topologically derived location. Often corresponds to living groups, whereas ancestrally featured stem groups attach near the cladogram's root or consist of the paraphyletic ancestral part of the tree. [2, 8]

darwin A rate of phenotypic evolution corresponding to a change by a factor of *e* per million years. [6]

developmental constraint A factor in development, such as an obligatory tissue interaction, that might prevent or channel an evolutionary change. [4]

directional selection Natural selection in which a monotonic shift in phenotypic value is favored. [3]

disruptive selection Natural selection in which an intermediate phenotypic value is in disfavor, causing increases in frequency of divergent phenotypes. [3]

downward causation In hierarchies, the case in which a change in a hierarchical level causes a concomitant change at a lower hierarchical level. [1]

duplicative transposition *See* **Transposable elements.**

ecological-evolutionary units A group of taxa that have predictable taxonomic composition but also are confined to a certain ecological milieu for some period of time. [7] *See* **coordinated stasis.**

effect hypothesis Notion that characters might proliferate in a biota as they hitchhike along with rapidly speciating clades. [6]

effective population size A complex estimate of the number of individuals in a population that contribute genes to subsequent generations. Effective population size increases with an increase in the number of breeding individuals, an equalization of the sex ratio, and an increase of the geometric mean of population size of successive generations. [3]

enhancer A nucleotide sequence at some distance from the structural gene that influences expression of the gene. [3]

epigenetic pleiotropy Condition when a given developmental event affects widely disparate parts of the overall phenotype. [4]

evolutionary eruption Preston Cloud's (1948) term for rapid appearance of an evolutionary radiation. [8]

evolutionary fauna A group of taxa, found (by means of factor analysis) to behave statistically independently of other groups in terms of temporal diversity trends. [7]

evolutionary systematics A school of classification that groups taxa on the basis of the two criteria of evolutionary relationship and the degree of phenotypic difference. [2]

exaptation The process by which a structure is co-opted by evolution to a new function. [5]

exon The nucleotide sequence of the structural gene that codes for the protein. It may be interrupted by introns. [3]

fitness The relative ability of different genotypes to leave offspring. [3]

frameshift mutation A mutation owing to a loss or gain of a small segment of DNA and a subsequent shift of the adjacent DNA sequence. [3]

frequency-dependent selection Natural selection whose strength and direction depends on the frequency of alleles of a locus in the population. [3]

functional constraint Non-random channeling of evolution, owing to natural selection acting to allow or enhance function. [4]

gene conversion The process by which a specific sequence of DNA is converted to resemble another sequence. [3]

gene flow The sum of successful dispersal and breeding of individuals originating in one population but arriving in another. [3]

genealogy A set of relationships among taxa, based on their evolutionary branching sequence. [2]

genetic drift The change in gene frequency, owing to random processes of gains and loss in a population. [3]

genetic pleiotropy The effect of a gene on more than one aspect of the overall phenotype. [3]

geographic stratigraphic completeness Proportion of the geographic range represented by the rocks containing a given fossil species. [6]

geometric morphometrics An approach to estimating form by means of the establishment of landmarks, standardization of forms to eliminate the effect of size, and statistical analysis of differences in landmark locations. [5]

Haldane's paradox Why does the rate of evolution in the fossil record appear to be so slow? [6]

heritability (broad-sense heritability) The proportion of phenotypic variance that can be explained by genetic variance. *See* **narrow-Sense heritability**. [3]

heterochrony A change in order of appearance of a trait during development between an ancestor and its evolutionary descendant. [4]

hitchhiking (species level) The process by which a character state increases in frequency among species, by virtue of its coincidental association with a group that is increasing or decreasing in species richness. [4]

homology Possession of a trait by two or more taxa because of a common evolutionary origin. [2]

homoplasy Possession of two or more taxa of a character state not because of a common evolutionary origin but because of convergence, parallel evolution, or evolutionary reversal. [2]

hopeful monsters Richard Goldschmidt's notion of hypothetical new mutants of major phenotypic difference that might give rise to strong evolutionary change in a population. [1]

***Hox* genes** Set of genes with a characteristic homeodomain sequence, all involved in regulation of transcription, important in developmental events, and found throughout the Metazoa. [4, 8]

intron A nucleotide sequence that is part of a structural gene but is not part of the DNA message that codes for the amino acid sequence of the protein. [3]

inversion A reversal of some part of a chromosome, relative to a reference chromosome. [3]

iterative evolution Repeated origin of evolutionary stocks of similar morphology. [6, 7]

key innovation A new genetically determined phenotype with strong potential for further evolutionary change. [5]

lethal gene A gene whose presence (usually in double dose in a homozygote) is lethal to the organism. [3]

Linnaean concept of species A species concept that idealizes the species by an essence, distinguishing it immutably from all other species. [3]

Lyellian curves Plots of the percentage of a fossil fauna that is still extant. Variants of this definition are common, such as percentage of a fossil fauna that is present some number of years after a reference time datum. [7]

macroevolution The sum of those processes that explain the character-state transitions that diagnose evolutionary differences of major taxonomic rank. [1]

macromutations Mutations of strong phenotypic effect. [1, 3]

mass extinction An extinction that is characterized by loss of many taxa in a geologically brief time period. Also thought of as a statistically significant and higher rate of extinction, relative to the background extinction over a longer time period. [7]

microevolution As commonly used, evolutionary change occurring within a species. [1]

microstratigraphic acuity Amount of time represented by a given sediment sample. [6]

Modern Synthesis A movement of evolutionary biology arguing that variation within natural populations must be studied to understand the overall evolutionary process, that species arise from changes in within-population variation, and that natural selection is preeminent in the formation of the phenotype. [1]

molecular clock Hypothesis that the rate of evolutionary change in DNA is constant over geologically long periods of time. [2, 3]

molecular drive Theory that argues that gene conversion, unequal crossing over, and duplicative transposition all contribute toward the construction of gene families. [3]

monophyletic group A group of species that includes a species (or a hypothesized ancestral species defined by a set of character states) and all of its descendants. [2]

morphogen A molecule that diffuses through, or is actively transported through, an embryo, providing a signal necessary for a developmental event to occur. [4]

morphological disparity The extent of morphological variation found for a given number of taxa. Estimates may be normalized by taxonomic level (e.g., disparity among genera within a phylum). [7, 8]

morphological species concept Division into species on the basis of morphological differences. [2]

mosaic evolution Case in which different sets of traits in an organismal lineage evolve at different rates and apparently independently of each other. [6]

mutation The set of processes that causes a change in a nucleotide sequence in an organism. [3]

narrow-sense heritability The proportion of phenotypic population variance that can be explained by additive genetic variation (variation that can be ascribed to among-allele differences). [3]

natural selection The process of change of gene frequencies in a population, owing to fitness differences among genotypes. [3]

neutral theory of molecular evolution Theory arguing that DNA sequence evolution is governed by stochastic processes and that molecular polymorphism is neutral with regard to fitness. [3]

paracentric inversion Inversion not including the centromere. [3]

paradigm structure Rudwick's optimality model that predicts an optimal structure for a function. [5]

parapatry The rise of regional genetic differentiation, despite some gene flow. [3]

paraphyletic group A group of species that includes the ancestral species but not all of the known descendant species. [2]

parsimony The use of the shortest number of evolutionary steps as a criterion for constructing a cladogram. [2]

peripatric speciation A hypothesis of speciation by budding off of small founder populations into geographically marginal, and usually ecologically marginal, areas. Such budding is accompanied by strong natural selection, genetic drift, and rearrangement of genetic determination of phenotypic traits. [3]

phenetics A theory and practice of classification involving grouping of taxa by virtue of their overall similarity. [2]

phenotypic plasticity Case in which a single genotype may be found in a range of phenotypes, usually as a response to differences in the environment. [3, 7]

phyletic evolution Evolutionary change within a lineage, without cladogenesis. [6]

phylogenetic systematics The area of study in which genealogies are established using cladistic methods. [2]

phylogeny A hypothesis of the evolutionary history of a group, including hypothesizing ancestors, and exact order and geographic locus of cladogenesis. [2]

pleiotropy *See* **genetic pleiotropy, epigenetic pleiotropy**. [3]

plesiomorphy The state in which two taxa share ancestral character states for lack of any divergent evolutionary change. [2]

point mutation A DNA mutation in which one nucleotide has been changed into another, with no change in overall number of sites. [3]

polymorphism The presence of variants, genetic or phenotypic, within a population. [3]

polytypism The situation in which a species consists of a series of geographically and phenotypically (or genotypically) distinct subpopulations. [3]

postmating isolation Isolation between members of two populations of a sexually reproducing organism, owing to difficulties in development or increased mortality in the zygote formed from the mating. [3]

premating isolation Isolation between members of two populations of a sexually reproducing organism where lack of recognition factors prevents mating from occurring. [3]

primary intergradation Case in which a cline is due to processes excluding a history of isolation and secondary contact. [3]

promoter A nucleotide sequence immediately "upstream" of the structural gene that is necessary for initiation of transcription. [3]

protein polymorphism A polymorphism in a population of different protein products of a locus. *See* **allozyme.** [3]

provinciality The degree to which a large regional biota can be broken up into statistically distinguishable geographic subunits. [7]

pseudoextinction The apparent extinction of a taxon, because it has evolved phyletically into another taxon that is sufficiently distinctive to been given a new taxonomic name. [6]

pseudogenes Nonfunctioning (and probably former) structural genes. [3]

punctuated equilibrium theory A theory that asserts that species do not change during most of their history but that change is mostly concentrated at speciation events. [1, 6]

quantum evolution A greatly increased rate of phyletic evolution over a relatively short period of time. [6]

reciprocal monophyly When separated, two populations may share the same gene lineages, but after a time, surviving gene lineages will differ between the isolated populations. [3]

reference time datum (RTD) A time horizon in the geological record, which is used as a starting point for the study of taxonomic survivorship, either forward or backward in time. [7]

regression In geological parlance, a lowering of sea level, explained either by a global fall of sea level, or a local rise of land elevation. [7, 8]

regulatory gene A gene whose product is a polypeptide that affects the degree of expression of a structural gene. [3]

Robertsonian fusion Fusion of two acrocentric chromosomes. [3]

RTD *See* **reference time datum.**

secondary contact After allopatric speciation, the reintroduction of contact between the offspring species by elimination of the geographic barrier. [3]

selection coefficient A fraction representing the proportional difference in fitness of one genotype relative to others. [3]

shifting balance theory Theory of interaction of gene flow, local population differentiation, and genetic drift. Genetic drift or intermittent gene flow permits a population to leave a local adaptive peak and climb a higher one. [3]

speciation The formation of two or more new species from one former species. [3]

species drift The increase or decrease of number of species in a taxonomic group owing to random speciation and extinction processes. [3]

species selection A change in the number of species in a taxonomic group owing to its deterministically different speciation or extinction rate. [3]

species stasis Lack of change in morphological characters of a species throughout its history. [6]

stabilizing selection Natural selection that favors the same genotype or phenotype throughout successive generations. [3]

stem group A taxon that is usually found to attach to a cladogram near the root and may be paraphyletic. [8]

step cline A cline with a relatively sharp change over a small amount of geographic distance, relative to very little change on either side of the step. [3]

stratigraphic completeness *See* **temporal stratigraphic completeness, geographic stratigraphic completeness.**

stratocladistics An approach by which cladograms are established from order of appearance of taxa in the fossil record. [2]

structural gene A gene whose product is a protein involved in cellular metabolism or at least does not act by binding to DNA and thereby directly regulate expression of other genes. [3]

sympatric When two populations or species are in sufficient contact for an opportunity for interbreeding to occur. [3]

sympatric speciation Division of a species into two or more offspring species in the absence of geographic isolation. [3]

synapomorphy A character state shared among two or more taxa but to no others outside of this group. [2]

taxic approach The use of named taxa, usually above the level of species, their geological ranges, and their geographic ranges to study rates of evolution and diversity changes. [6, 7]

taxonomic longevity The time over which a given taxon lives. [7]

taxonomic survivorship curve A plot in which longevities of all taxa in a group are considered as if they were life spans of a group of individuals. Life spans are aggregated into a cohort and a survivorship curve is plotted as if they all were born at the same time. [7]

temporal scope The period of time represented by a given column of rock. [6]

temporal stratigraphic completeness The proportion of geological time of the total temporal scope represented by the preserved rock column. [6]

total evidence hypothesis Hypothesis that the most accurate cladograms will be obtained by analyzing all available combined evidence (e.g., molecular and morphological characters), as opposed to examining trees constructed from specific data types or calculating consensus trees from individual trees derived, respectively, from individual data types. [2]

transcription factor A molecule that influences the rate of transcription of a gene. [4]

transgression A deepening of water at a site, owing to either a rise in sea level or a local fall of the sea bed. [5, 6]

transilience mechanisms of speciation Speciation mechanisms that involve changes in genetic organization, such as polyploidy. [3]

transposable elements DNA sequences that are capable of moving from one part of the nuclear DNA to another or are capable of producing a replicate that can move to another site (duplicative transposition). [3]

truncation selection Natural selection that eliminates all individuals beyond a given phenotypic value. [3]

upward causation In hierarchies, the case in which a change in a lower hierarchical level has an effect on higher levels. [1]

Vendian The last part of the Neoproterozoic, in which bona fide animal fossils appear in great abundance. [7, 8]

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