SECTION I

THE ORIGINS OF BIOLOGICAL DIVERSITY

Evolutionary biologists have much to explain. Our planet is occupied by a few million species of organisms. Impressive as the numbers are, they represent a few percent at most of all species that have ever lived. Where have the contemporary ones come from, why have all the rest gone, and why have the few, and no others, remained? How did a single species, *Homo sapiens*, come to dominate a planet that started out 4.567 billion years ago without any living organisms whatever? Answering questions such as these is part of the exciting task of accounting for the origin of life, the origin of species, their multiplication, diversification, and elaboration, and their extinction. This enormous challenge is being met by combinations of specialists in a broad range of disciplines, from microbiology and biochemistry to paleontology. What once looked like a linear array of experts at the forefront of science now appears to be a circle: molecular biologists and paleontologists have a common purpose, and together with ecologists, physiologists, geneticists, systematists, and others, jointly attempt to understand the origin and proliferation of life. This book is a reflection of that joint effort in the early part of the twenty-first century.

The first section is devoted to evolutionary history. It begins (chapter 1) with a broad view of the first 3 billion years of life, and presents the problem of trying to understand how the environment shaped the timing and pattern of evolution from the simplest organisms to the most complex. Years ago G. Evelyn Hutchinson wrote a book entitled *The Ecological Theatre and the Evolutionary Play*. The ecological theater changes, from scene to scene, and change largely explains both why evolution occurs and the directions it takes. In chapter 1, Andy Knoll and David Johnston extend the framework by making a distinction between an environmental (abiotic) and an ecological (biotic) context of evolution in order to focus on the physico-chemical component of the theater. They survey the biochemical evidence of conditions in the marine environment from about 2.5 to less than a billion years ago, and conclude that the deep history of life can only be understood by appreciating the dynamic nature of the physical environment. Organisms alter their environment, by releasing oxygen and depositing carbon for example; therefore, it is best to think of the whole drama of the history of life as being a tale of mutual interactions. These points are made in explaining why long periods of relatively little change such as the gradual rise in atmospheric oxygen are followed by relatively rapid transitions to new states. In more ways than one the chapter sets the stage for the rest of the book.

A time-honored method of identifying probable causes of evolution is to find trends and to search for features of the environment that are associated or correlated with them. In chapter 2, David Jablonski first gives guidance on how to interpret trends in body size and the accumulation of species in clades. This is an important overview because trends can arise in different ways. Working backwards in time to reconstruct a phylogeny, and then forward to narrate the history of a clade, he is able to identify where and how it evolved and diversified along two environmental axes: onshore-offshore gradients and tropical-temperate zone contrasts. With regard to the first, he finds that new taxa of marine invertebrates arise mostly in onshore habitats: clades that start in shallow water stay there or go deep, whereas those that start in deep water stay there. With regard to the second, he finds a strong tendency for clades to originate in the tropics and persist there for a long time. A net flow out of the tropics is caused not by species spreading from one climatic zone to another but by staying in one and giving rise to another species in a neighboring zone. This pattern raises questions about environmental determinants and the geography of speciation that are addressed later in the book (chapters 13 and 14). A major conclusion of this chapter is that the unfolding patterns of species diversity cannot be explained solely by microevolution. Clades have unequal histories and fates, and this leaves a macroevolutionary imprint on the product of microevolution.

Some faunas have had a disproportionate influence on our thinking about evolution, because they are so unusual. The Burgess Shale fauna from the Cambrian are a case in point, because they proliferated extravagantly and rapidly from poorly known, apparently impoverished, beginnings. Some taxonomic groups have the same iconic status because they too offer tantalizing paleontological puzzles. Everyone's favorite is the dinosaurs. This clade of theropod reptiles had an extraordinary history and fate. It captures our attention because of the striking diversity in form, the unequaled size of the largest members, and its rapid disappearance. These features demand an explanation. At one time the biggest question was why, having prospered, did they become extinct so rapidly? Answering this question, by invoking a major perturbation to the Earth's climate caused by a meteorite collision, removed a veil from another, perhaps more fundamental, question: who, exactly, are dinosaurs? In chapter 3, Phil Currie offers a narrative account of how modern phylogenetic and anatomical research has cast these animals in a fundamentally new light, and concludes they are still alive, represented solely by a group we call birds. Feathers, which once seemed to be unique to birds, are now known to have been possessed by their theropod ancestors. A little more than a decade of research on fossils from China has revealed numerous examples of feathers in various stages of evolutionary elaboration up to the form in *Archaeopteryx* that permitted flight. It will take time for everyone to feel comfortable with the idea of having a dinosaur in a bird cage in their living room.

Fossils are a luxury. Most evolutionary biologists don't have them, but increasingly they do have molecular tools for reaching deeply into the past to reconstruct the phylogenetic and demographic history of living organisms. Inferring phylogenetic history has become standard practice for many ecologists and behaviorists (chapters 12–16), so it is fitting to have a chapter that serves as an exemplar of what can be learned about the past without having a single fossil. It conveys the excitement of a field of inquiry undergoing rapid change as new and more powerful genomic and statistical tools become available. Scott Edwards's group (Balakrishnan et al.; see chapter 4) review the progress made on the question of how to use information on genetic variation (polymorphisms) to reach a reliable estimation of genetic relationships between populations, that is, to determine affinities in time and space. Using birds as an example, they consider why populations share polymorphisms for so long, the population-genetic context of their evolution, the way in which they can be used to construct species trees as opposed to gene trees, and the implications all of these have for efforts to identify and characterize species (see chapter 13). For example, they argue against the idea that nuclear genes are less useful for delimiting species than are mitochondrial genes. The authors conclude with expectations of future developments and recommendations for those who work with birds.