Aim and Scope of the Book

"Nothing in biology makes sense except in the light of evolution"
—Teodosius Dobzhansky

EVOLUTIONARY BIOLOGY DESCRIBES THE HISTORY OF LIFE AND EXPLAINS WHY ORGANISMS ARE THE WAY THEY ARE

OUR WORLD IS FILLED WITH AN extraordinary diversity of living organisms (Fig. A&S.1). The Sun's light is harvested by bacteria, algae, and plants, and every feasible source of chemical energy, from hydrogen gas to carbon monoxide, is exploited by some microbe. Life thrives in the most extreme environments, from Antarctic rocks to scalding undersea vents to crevices miles beneath the Earth's crust. Organisms are sensitive to the slightest variations in their environment: Bacteria find their way by sensing the Earth's magnetic field, moths find their mates from a few molecules' scent, and owls see their prey from afar on a moonless night. Birds can use specialized tools to help them extract food, bees coordinate the activity of their hive, and human societies use language and technology to overcome the limitations of their biology.

All of these diverse functions are achieved by the same fundamental biochemical system. Genetic information stored in the sequence of bases in DNA is **transcribed** into RNA and then **translated** into sequences of amino acids that construct and maintain the organism. The engineering of organisms is as remarkable as its consequences. DNA sequences can be replicated with less than one error in a billion bases. Proteins at ambient temperatures can catalyze reactions that human chemists can achieve only under extreme conditions and with much coarser specificity. Interactions between DNA and proteins regulate precise patterns of gene expression that allow the reliable construction of complex organs, including, most impressively, the human brain, which generates and controls elaborate behavior. All of this is determined by a remarkably compact genome; the human DNA sequence, for example, encodes less information than is stored in a personal computer.

We know, at least in outline, how the DNA sequence is translated into proteins, how these proteins affect metabolism and regulate gene expression, and how multicellular organisms develop reliably from a single cell. We also know, at least in outline, how the diverse organisms now living came to be. All of them (including us) descended from one "universal ancestor" that lived about 3.5 billion years ago. That ancestor itself descended from a much simpler organism in which RNA carried out the present roles of both DNA and protein. Thus, all the biochemical, morphological, and behavioral diversity around us descended from a few original genes.

The exquisite biological devices that we now see appear as though carefully designed

FIGURE A&S.1. Diversity of adaptation. *Top row*: Life in extreme environments. Organisms can live in the very cold environment of Antarctic dry valleys (*left*) or in hydrothermal vents deep within the sea (tube worm community; *right*). *Middle row*: Diversity of morphological adaptation. The fine structure of moth antennae (*left*) allows the detection of just a few molecules of pheromone. The large eyes of the vermiculated screech owl (*Otus guatemalae; right*) allow it to find prey at night. *Bottom row*: Behavioral adaptation. The New Caledonia crow (*Corvus moneduloides*; *left*) fashions tools for specific purposes, here to extract insects from holes in a tree branch. Honey bees (*Apis mellifera; right*) live and work in an organized "society" with specific tasks assigned to maintain the hive.

for their present purposes, and this appearance of design was long taken as evidence of an intelligent creator. We now know that biological function is constructed and maintained by natural selection: the gradual accumulation of variations that arise by chance and that are preserved because they aid the survival and reproduction of their carriers. The theory of evolution is a synthesis of Darwinian natural selection and Mendelian genetics. It allows us to ask not just how life evolved, but why it is as it is: Why do organisms develop from a single cell?; Why is the genetic code as it is?; and Why is there sexual reproduction?

EVOLUTIONARY BIOLOGY IS A VALUABLE TOOL

Our understanding of the history of life and the mechanism by which life has evolved has influenced virtually every aspect of human society from literature to medicine. However, evolutionary biology is not simply a historical science. Information on evolution and the application of principles learned from the study of evolution also have many practical uses in fields as diverse as geology, computer science, and epidemiology. We give here three examples.

Because closely related organisms tend to have similar features, evolutionary classification can help predict the biology of an organism through comparison with its relatives. Traditionally, microorganisms are studied by isolating them in culture. However, the great majority of microbes cannot at present be grown in the laboratory. By combining tools from molecular and evolutionary biology, genes from unculturable species can be cloned and analyzed to provide the information that places them into the tree of life. This allows scientists to infer much about these unculturable microbes, such as details of their metabolic processes or their interactions with other organisms.

This approach has led to the development of new drugs for treating malaria and related diseases. Malaria is caused by the infectious parasite *Plasmodium falciparum*. Traditional antimalaria drugs that kill *P. falciparum* are frequently quite toxic to humans, because they attack pathways common to eukaryotes. In the 1970s, scientists found an unusual **organelle** in *P. falciparum* that contained its own DNA. Much to their surprise, evolutionary trees based on genes in this DNA indicated that this organelle (the apicoplast) was closely related to plant **chloroplasts** (Fig. A&S.2). Plant chloroplasts originated from an **endosymbiosis** between ancestors of plants and a bacterium related to modern day **cyanobacteria** (**Chapter 8**). Evolutionary analysis has shown that the *Plasmodium* lineage obtained this plastid by entering into a symbiosis with another eukaryote (most likely an alga) that contained a plastid. Although many of the features of this algal-like symbiont have since been lost, the plastid was maintained, and although *Plasmodium* does not carry out photosynthesis, the metabolic functions of the apicoplast are essential for its survival. The absence of the apicoplast metabolic pathways in mammals has suggested new targets for antiparasite medications. A variety of antibiotics, enzyme inhibitors, and herbicides that target the apicoplast show promise at killing *P. falciparum* and relatives that cause toxoplasmosis and cryptosporidiosis.

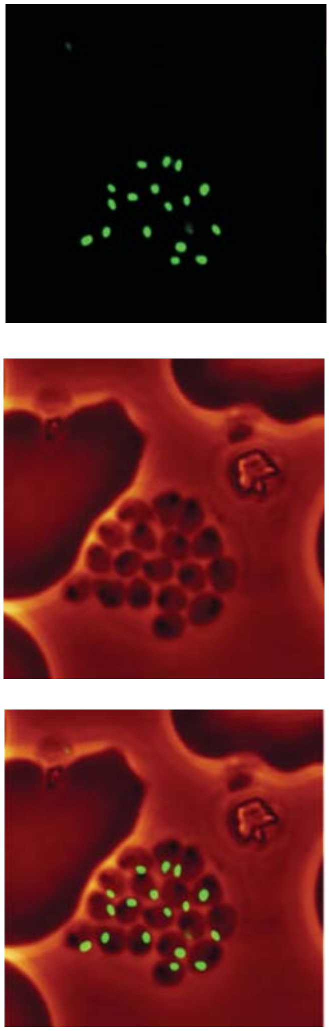

FIGURE A&S.2. Apicoplasts are visible through the use of green fluorescent protein (*top*); round balls in center are malaria parasites (*middle*); and green apicoplasts inside parasites (*bottom*).

Evolutionary biology has also been very useful in enhancing our understanding of macromolecular structure. This is perhaps best shown through studies of **ribosomal RNA** (rRNA). In all organisms, rRNA is involved in the translation of messenger RNA into proteins. rRNA molecules form intricate structures, driven in part through internal base pairing, much like the base pairing that forms the DNA double helix (Fig. A&S.3). Biochemical analysis of rRNA molecules has been unsuccessful in solving the rRNA folding problem, partly because there are simply too many base-pair combinations to test. Until recently, structural studies have also been unsuccessful, because rRNA molecules do not readily form the crystals needed to solve structures by X-ray diffraction. However, the base pairings within rRNA molecules have been determined by tracing the evolutionary history of nucleotide changes and identifying cases in which changes occurred in two separate parts of the molecule at the same time. By identifying thousands of these correlated changes, researchers have been able to determine which nucleotides base pair with each other (**Chapter 19.21**).

Numerous human endeavors have benefited from our understanding of how evolution works. Animal and plant breeding programs are continually improved through the application of principles of population genetics. Similar approaches are being used in biotechnology, through the use of so-called molecular breeding (**Chapter 17.1.1**). One example is the creation of designer proteins that have new or en-

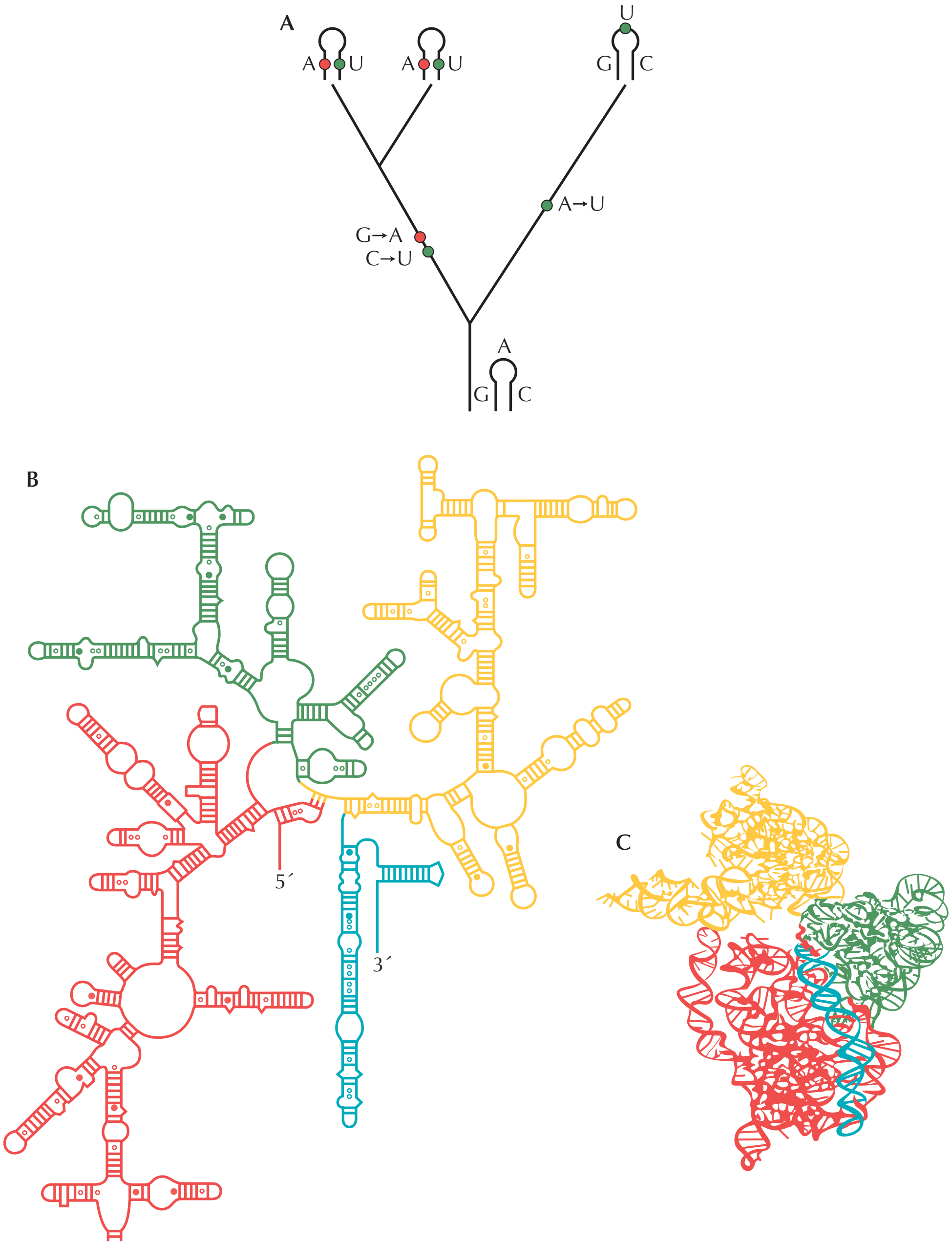

FIGURE A&S.3. The pattern of evolutionary change in an RNA molecule can be used to determine its structure. (*A*) Where two parts of the RNA molecule pair, a change in one base must be accompanied by a change in its partner if pairing is to be maintained (e.g., G→A [*red*] and C→U [*blue*]). This maintains the pairing between these bases. In contrast, changes in unpaired regions can occur independently (e.g., the single change A→U [*green*]). (*B*) The secondary structure of the 16S ribosomal RNA molecule was inferred using this method, based on comparisons between more than 7000 sequences from different bacterial species. Ladders indicate paired helices. (*C*) The full three-dimensional structure of crystals of the molecule was determined directly in 2000 and confirms the inference made by the comparative method: More than 97% of the predicted pairs were found in the crystal structure. Different colored regions in *B* and *C* correspond to different domains of the molecule.

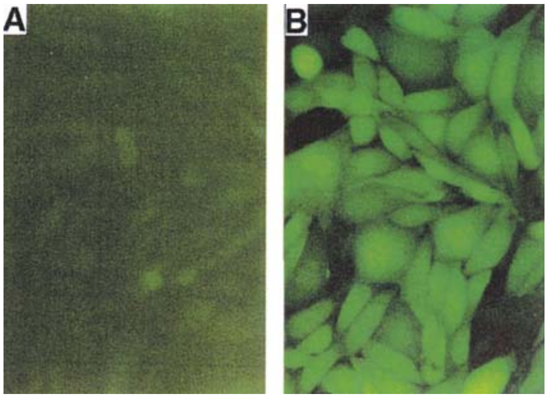

FIGURE A&S.4. Molecular evolution can be used to solve a complex practical problem. Here in vitro selection of a synthetic green fluorescent protein (GFP) gene (*B*) was used to increase its signal over wild type (*A*).

hanced functions. Fluorescent proteins are very useful tools in biological research (e.g., Fig. A&S.2). They are detected using fluorescence microscopy and other light-sensitive instruments through the light emitted by the proteins when placed under the proper conditions. To make the best use of fluorescent proteins, it is helpful to have different forms that emit different colored light. The original green fluorescent protein was isolated from a jellyfish species, *Aequorea victoria*. Using in vitro molecular breeding methods, scientists have altered the green fluorescent protein, creating new versions that fluoresce at other wavelengths. Molecular breeding methods rely on our understanding of the mechanisms of evolution to enable designer macromolecules to be created (Fig. A&S.4). In nature, the evolution of new functions for, say, a protein may be limited by the likelihood that the appropriate genes carry the necessary combination of mutations. **Recombination** (which is used deliberately in molecular breeding) brings together different mutations and greatly increases the efficiency of in vitro selection (see **Chapter 23.x**).

MOLECULAR BIOLOGY AND EVOLUTIONARY BIOLOGY ARE OVERLAPPING FIELDS OF STUDY

Molecular biology and evolutionary biology are both thriving fields. Over the last half-century, however, they have largely developed independently of each other. Of course, evolutionary biology uses many molecular techniques and investigates molecular as well as morphological and behavioral variation. Conversely, molecular biology uses (at least implicitly) evolutionary methods to establish relationships between organisms and between genes and to distinguish functional sequences. Nevertheless, the two fields remain as largely separate communities and ask rather different questions. Our aim in this book is to explain evolutionary biology in a way that will be accessible—and interesting—to molecular biologists and to show how evolutionary methods bear on some of the most recent molecular discoveries.

Part I provides a historical discussion of the two fields, outlining key advances and concepts. The overwhelming evidence for evolution is presented, including arguments supporting natural selection as its central mechanism. Part II presents an overview of the diversification of life. Beginning with the origins of life more than 3 billion years ago, this part shows how the three domains of life—bacteria, archaea, and eukaryotes—have diversified. We describe the evolution of multicellular organisms, both as seen in the fossil record and through our recent understanding of developmental programs. Part II lays the groundwork for Part III, which explains the nature of genetic variation, the mechanisms of evolution, and their consequences. Almost all populations contain abundant variation, which is generated by mutation and recombination. This variation is seen both at the level of DNA and protein sequence and in the morphology and behavior of the whole organism—traits that depend on the interaction between large numbers of genes. Natural selection acts on this variation and is responsible for the remarkable adaptations that we see in the living world. We show how the various evolutionary mechanisms interact with each other to generate these adaptations, to produce diverse species, and to shape the genetic system itself. Part IV closes the book with a discussion of the evolution of our own species and the role that evolution and evolutionary biology now play in human endeavors.

This textbook is supported by a comprehensive Web site, which includes two chapters on the quantitative methods that are used to study evolution. The first presents tools used to reconstruct phylogenies; the second is a detailed introduction to evolutionary modeling. The Web site also includes notes that give full references, expands on some of the arguments in the main text, and provides links to other useful Web sites. Combined with the recommended reading list found at the end of every book chapter, this will guide the student into the extensive literature of evolutionary biology and will provide useful background material for the instructor. Finally, the Web site includes problems and worked examples that are associated with the chapters in Part III.

We hope that, as well as providing a clear explanation of biological evolution, our book will help to bring molecular and evolutionary biology closer together. The past century has seen extraordinary advances in both branches of biology, and the coming decades promise to be still more exciting.

http://evonet.org is a Web site that provides a good overview of evolutionary biology.

Meagher T.R. and Futuyma D. 2001. Evolution, science, and society. *Am. Nat.* **158:** 1–46.
Examples of how evolutionary biology can be applied in diverse ways. Also available from http://evonet.sdsc.edu.evoscisociety/.