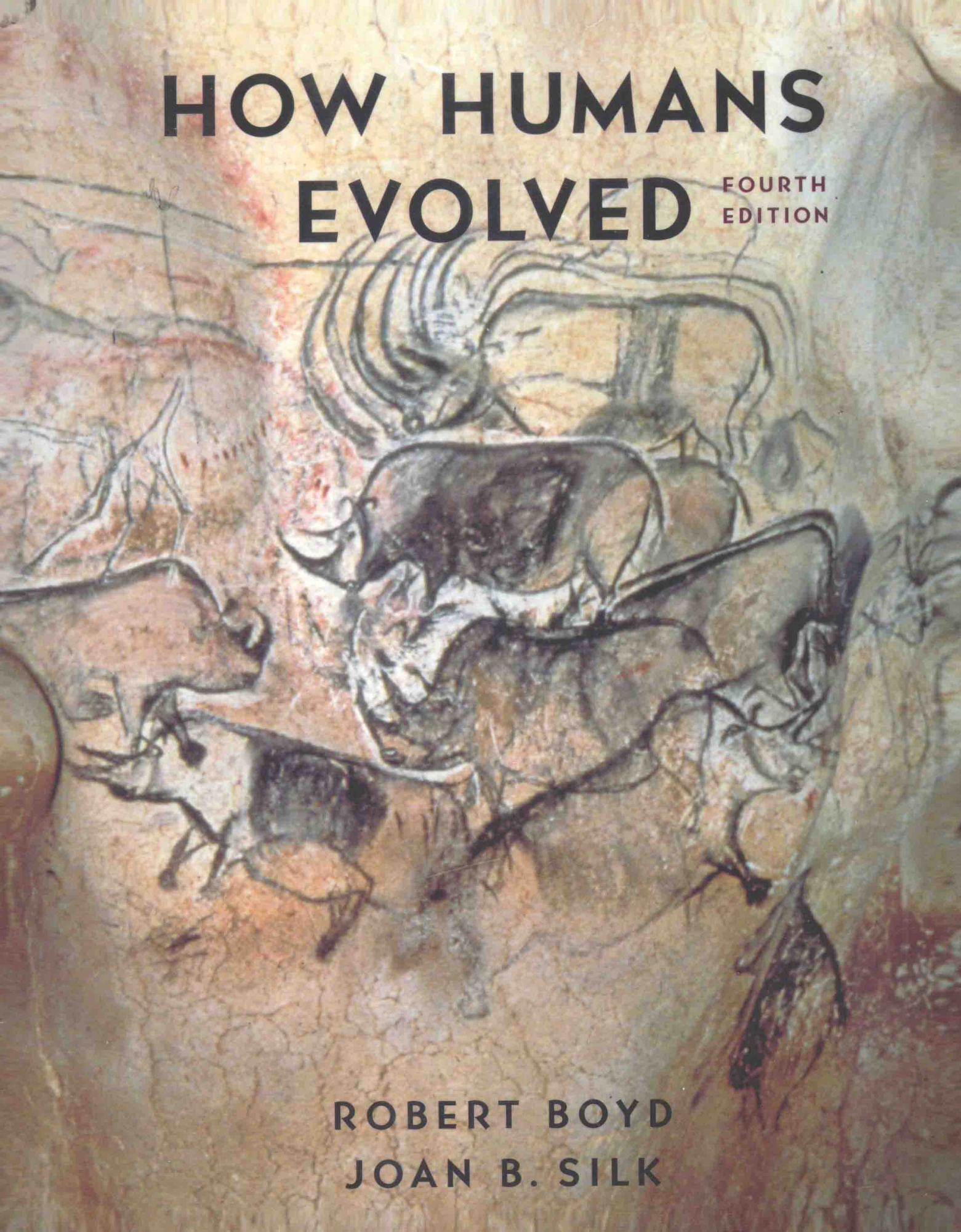
HOW HUMANS EVOLVED

FOURTH EDITION



ROBERT BOYD
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HOW HUMANS EVOLVED

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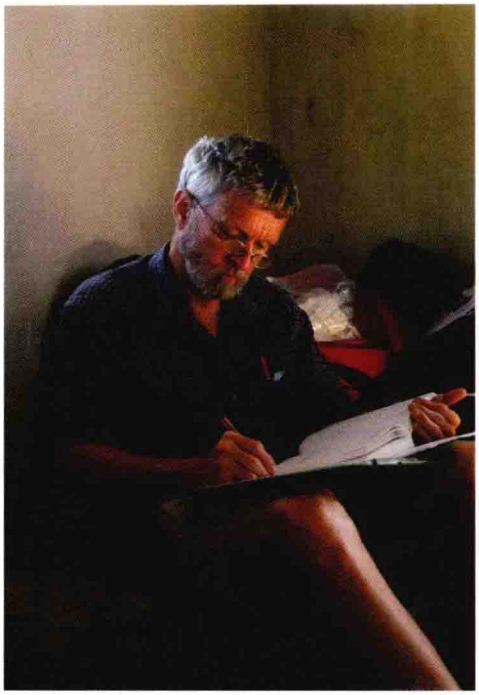
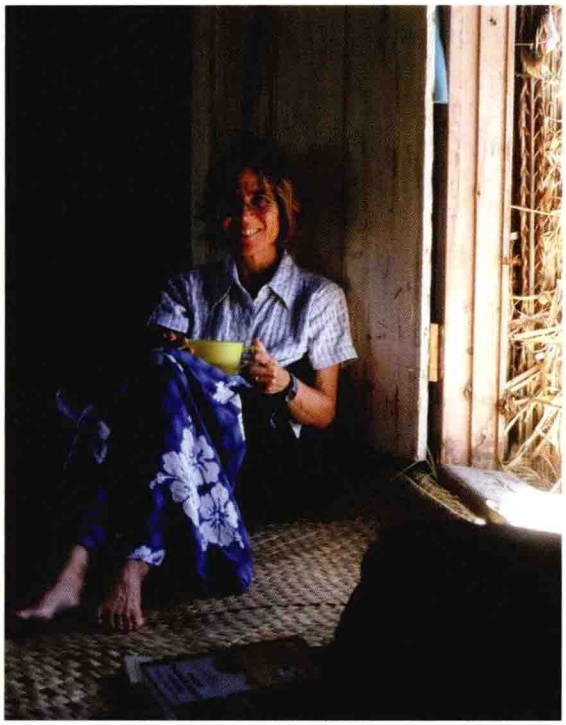


ROBERT BOYD has written widely on evolutionary theory, focusing especially on the evolution of cooperation and role of culture in human evolution. His book, Culture and the Evolutionary Process, received the J. I. Staley Prize. He has also published numerous articles in scientific journals and edited volumes. He is currently co-director of the MacArthur Preferences Network and Professor of Anthropology at the University of California, Los Angeles.

JOAN B. SILK has conducted extensive research on the social lives of monkeys and apes, including extended field work on chimpanzees at Gombe Stream Reserve in Tanzania, and baboons in Kenya and Botswana. She is also interested in the application of evolutionary thinking to human behavior, especially adoption and friendship. She has published over 60 papers in scientific journals and scholarly edited volumes, and is currently Professor of Anthropology at the University of California, Los Angeles.



PREFACE

How Humans Evolved focuses on the processes that have shaped human evolution. This approach reflects our training and research interests. As anthropologists, we are interested in the evolutionary history of our own species, *Homo sapiens*. As evolutionary biologists, we study how evolution works. In this book, we integrate these two perspectives. We use current theoretical and empirical work in evolutionary theory, population genetics, and behavioral ecology to interpret human evolutionary history. We describe the changes that have occurred as the hominin lineage has evolved, and we consider why these changes may have happened. We try to give life to the creatures that left the bones and made the artifacts that paleontologists and archaeologists painstakingly excavate by focusing on the processes that generate change, create adaptations, and shape bodies and behavior. We also give serious attention to the role of evolution in shaping contemporary human behavior. There is considerable controversy about evolutionary approaches to human behavior within the social sciences, but we think it is essential to confront these issues openly and clearly. Positive responses to the first three editions of *How Humans Evolved* tell us that many of our colleagues endorse this approach.

One of the problems in writing a textbook about human evolution is that there is considerable debate on many topics. Evolutionary biologists disagree about how new species are formed and how they should be classified; primatologists argue about the adaptive significance of infanticide and the effects of dominance rank on reproductive performance; paleontologists disagree about the taxonomic relationships among early hominin species and the emergence of modern humans; and those who study modern humans disagree about the meaning and significance of race, the role of culture in shaping human behavior and psychology, the adaptive significance of many aspects of modern human behavior, and many other things. Sometimes multiple interpretations of the same data can be defended; in other cases, the facts seem contradictory. Textbook writers can handle this kind of uncertainty in two different ways. They can weigh the evidence, present the ideas that best fit the available evidence, and ignore the alternatives. Or they can present opposing ideas, evaluate the logic underlying each idea, and explain how existing data support each of the positions. We chose the second alternative, at the risk of complicating the text and frustrating readers looking for simple answers. We made this choice because we believe that this approach is essential for understanding how science works. Students need to see how theories are developed, how data are accumulated, and how theory and data interact to shape our ideas about how the world works. We hope that students remember this long after they have forgotten many of the facts that they will learn in this book.

NEW IN THE FOURTH EDITION

Many users of the book have found that it is hard to cover all of the material in a single quarter or semester. In response to this concern, we have put the book on a diet. Diets are hard because you have to give up things that you like. In this case, we eliminated the

chapter on language and the chapter on the human life cycle. We incorporated some material about the evolution of language in Part Four and some of the material about primate life history in Part Three. Readers familiar with previous editions will also notice that the readings are gone. Few of the instructors who were asked to review the third edition of the book seemed to think that the readings were essential. Removing them reduces the length of the book and helps streamline the text.

The study of human evolution is a dynamic field. No sooner do we complete one edition of this book than researchers make new discoveries that fundamentally change our view of human evolution. These kinds of discoveries include the spectacular fossil finds that reveal new chapters in human ancestry, new data that alter our interpretation of the behavioral strategies of primates, and experimental studies that reveal cross-cultural regularities in mating preferences. New developments in human evolutionary studies require regular updates of the textbook. Although we have made many changes throughout the book, readers familiar with prior editions will find significant changes in Parts II (Primate Behavior and Ecology), III (The History of the Human Lineage), and IV (Evolution and Modern Humans).

In Part I, we expanded Chapter 1 to provide more examples of the power of natural selection. We describe recent work which documents the rapid evolution of a complex placenta-like organs independently in several species of a single fish genus In Chapter 2, we provide expanded coverage of molecular genetics, and discuss more fully the role of proteins, gene regulation, and cell differentiation in development. Sometimes less is more: in Chapter 4 we have streamlined and updated the discussion of measuring genetic distance using sequence data rather than hybridization data.

In Part II, we revised a number of chapters to include recent empirical findings. For example, in Chapter 7 we discuss new evidence about the function of male-female relationships in baboons, and in Chapter 8 we describe new work on paternal kin recognition. We rewrote Chapter 9 entirely, integrating our discussion of the evolution of life history strategies (formerly covered in Part IV) with our discussion of the evolution of cognitive abilities in primates. These changes are prompted by new theoretical models that consider why evolution favored enhanced cognitive abilities in the primate order, and explore the consequences of these changes on primate life histories.

We have thoroughly revised Part III to incorporate a number of important findings that have substantially altered our understanding of human history. We rewrote Chapter 10 to include new data on the origin of primates, new fossils that tell us more about the New World primate radiation, and important new work on the the Miocene apes. In Chapter 11, we integrate information on *Sahelanthropus tchadensis* and *Orrorin tugenensis* into our discussion of the earliest hominins, and in Chapters 11 and 12, we describe new findings about the rate of development in early hominins. The tiny hominins from Flores, Indonesia—*Homo floresiensis*—make their first appearance in this edition in Chapter 13. We also discuss some new information about global climate change that may have influenced human evolution. Chapter 14 includes a new section on the earliest African *H. sapiens,* including Herto fossils and the redating of Omo Kibish I, and a new section on what genetic sequence data from modern populations (and from Neanderthals) can tell us about human evolution.

Part IV has been reorganized to provide a more integrated view of human diversity and contemporary behavior. Chapter 15 considers the sources of variation within and between human populations, and describes new findings that are relevant to understanding the processes that underlie human diversity. We have rewritten Chapter 16 to provide a more integrated view of how evolution shapes modern human

behavior. We have eliminated the dichotomy between evolutionary psychology and evolutionary anthropology, focusing instead on the insights evolutionary theory provides about modern human minds and behavior. We have also included information about the evolution of language and the adaptive significance of culture in this chapter. Chapter 17 includes new data on how evolution shapes mate choice and mating tactics in men and women, a more comprehensive discussion of the factors that influence mens' investment strategies, and a broader review of evidence about the investment patterns of stepparents and grandparents.

Throughout the book, we updated the list of references for further reading, and added a number of new study questions that are related to new material in the text. With the help of our colleagues and excellent copy editor, we also corrected a number of errors that found their way into the third edition.

We wrote this book with undergraduates in mind, and we have designed a number of features to help students use the book effectively. We have retained the "key idea" statements (now printed in blue type), and we recommend that students use these key ideas to keep track of important concepts and facts, and to structure their reviews of the material. Important terms that may be unfamiliar are set in bold type and defined in the text when they first appear. Readers can also find definitions for these terms in the Glossary. Discussion questions appear at the end of each chapters. These questions are meant to help students synthesize material presented in the text. Some of the questions are designed to help students review factual material, but most are intended to help students to think about the processes or theoretical principles they have learned. Some questions are open-ended and meant to encourage students to apply their own values and judgment to the material presented in the text. Students tell us that they find these questions useful as they attempt to master the material and prepare for exams. The list of references for further reading at the end of each chapter provides a starting point for students who want to delve more deeply into the material covered in that chapter.

The book is richly illustrated with photographs, diagrams, figures, and graphs. These illustrations provide visual information to complement the text. For some subjects, a picture is clearly worth 1000 words—no amount of description can enable students to conjure up an image of an aye-aye or appreciate the how much more similar the australopithecine pelvis is to the modern human pelvis than to the chimpanee pelvis. The diagrams of evolutionary processes that appear in Part I, are designed to help students visualize how natural selection works. The figures depicting the hominin fossils are drawn to scale, so each is presented in the same orientation and to the same scale. This should help students compare one hominin specimen with another. We have often been advised that you cannot put graphs in an undergraduate textbook, but we think that the graphs help students understand the evidence more fully. For us, it is easier to remember data that is portrayed graphically, than to recall verbal descriptions of results.

In addition, students can consult the multimedia guide to the fossil record, *Human Evolution* by Philip L. Walker and Edward Hagen, that is packaged with the text. This student resource offers lesson modules that illustrate controversies, archeological discoveries, and the anatomical differences between members of the nonhuman primate and human lineage, including prosimians, monkeys, apes, and hominins. The modules contain a photographs, drawings, and artwork plus a number of three dimensional animated specimens that can be "zoomed" to half-scale. Multiple-choice quizzes conclude each of the lessons.

ANCILLARY MATERIALS

For instructors, there is an instructor's manual and test-item file, which include a detailed outline of each chapter, answers to all of the discussion questions, and a bank of exam questions. The test questions are also available on CD in MS-DOS and Macintosh formats, and will be provided free of charge upon adoption of this textbook. For instructor use we also offer a media library of full-color transparencies of the figures and a CD containing many of the figures and photographs. This media library, available to adopting instructors, is especially rich, offering images not only from *How Humans Evolved*, but also from two other fine and well-illustrated books, Dean Falk's *Primate Diversity* and Glenn Conroy's *Primate Evolution*.

ACKNOWLEDGMENTS

Over the last 10 years, many of our colleagues have provided new information, helpful comments, and critical perspectives that have enriched this book. We are grateful for all those who have responded to our requests for photographs, clarifications, references, and opinions. For the fourth edition, Laura MacClatchy provided help with the Miocene apes in Chapter 10, Dan Fessler and David Schmitt gave us access to material for Chapter 16, and Kermyt Anderson dug up original data for figures in Chapter 17. Steven Reznik reviewed our discussion of the rapid evolution of placentas in the minnows he studies and kindly provided an image. Leslie Aiello helped with our discussion of hominin developmental rates. For help with the third edition, we thank Carola Borries, Colin Chapman, Richard Klein, Cheryl Knott, Sally McBrearty, Ryne Palombit, Steve Pinker, Karin Stronswold, and Bernard Wood. For help with the second edition, we also thank Tom Plummer, Daniel Povinelli, Beverly Strassman, and Patricia Wright. We remain grateful for the help we received for the first edition from Leslie Aiello, Monique Borgerhoff Mulder, Scott Carroll, Dorothy Cheney, Glenn Conroy, Martin Daly, Robin Dunbar, Lynn Fairbanks, Sandy Harcourt, Kristin Hawkes, Richard Klein, Phyllis Lee, Nancy Levine, Jeff Long, Joseph Manson, Henry McHenry, John Mitani, Jocelyn Peccei, Susan Perry, Steve Pinker, Tom Plummer, Tab Rasmussen, Mark Ridley, Alan Rogers, Robert Seyfarth, Frank Sulloway, Don Symons, Alan Walker, Tim White, and Margo Wilson.

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Richard Klein provided us with many exceptional drawings of fossils that appear in Part Three—an act of generosity that we continue to appreciate. We also give special thanks to Neville Agnew and the Getty Conservation Institute, which granted us permission to use images of the Laetoli conservation project for the cover of the second edition.

Many users of the book have commented on the quality of the illustrations. For this we must thank the many friends and colleagues who allowed us to use their photographs: Bob Bailey, Carola Borries, Colin Chapman, Nick Blurton Jones, Sue Boinski, Monique Borgerhoff Mulder, Richard Byrne, Scott Carroll, Marina Cords, Diane Doran, Robert Gibson, Peter Grant, Kim Hill, Kevin Hunt, Lynne Isbell, Charles Janson, Alex Kacelnik and the Behavioral Ecology Research Group, Nancy Levine, Carlão Limeira, Joe Manson, Frank Marlowe, Laura MacLatchy, Bill McGrew, John Mitani, Claudio Nogueira, Ryne Palombit, Susan Perry, Craig Stanford, Karen Strier, Alan Walker, Katherine West, and John Yellen. The National Museums of Kenya kindly allowed us to reprint a number of photographs.

We also acknowledge the thousands of students and dozens of teaching assistants at UCLA who have used various versions of this material over the years. Student evaluations of the original lecture notes, the first draft of the text, and the first three editions were helpful as we revised and rewrote various parts of the book. The teaching assistants helped us identify many parts of the text that needed to be clarified, corrected, or reconsidered.

We thank all the people at Norton who helped us produce this book, particularly our outstanding editor Leo Wiegman. We are grateful to our excellent copy editor, Stephanie Hiebert, for her relentless pursuit of clarity, accuracy, and typographical errors. We also thank Christopher Granville, who saw the book through production; and Elizabeth Erhart at Texas State University, San Marcos for preparing the revised instructor's manual.

PROLOGUE

WHY STUDY HUMAN EVOLUTION?

> Origin of man now proved—Metaphysics must flourish—He who understand baboon would do more toward metaphysics than Locke.
>
> —Charles Darwin, *M Notebook*, August 1838

In 1838, Charles Darwin discovered the principle of evolution by natural selection and revolutionized our understanding of the living world. Darwin was 28 years old, and it was just two years since he had returned from a five-year voyage around the world as a naturalist on the HMS *Beagle* (Figure 1). Darwin's observations and experiences during the journey had convinced him that biological species change through time and that new species arise by the transformation of existing ones,

and he was avidly searching for an explanation of how these processes worked. In late September of the same year, Darwin read Thomas Malthus's *Essay on the Principle of Population*, in which Malthus (Figure 2) argued that human populations invariably grow until they are limited by starvation, poverty, and death. Darwin realized that Malthus's logic also applied to the natural world, and this intuition inspired the conception of his theory of evolution by natural selection. In the intervening century and a half, Darwin's theory has been augmented by discoveries in genetics and amplified by studies of the evolution of many types of organisms. It is now the foundation of our understanding of life on Earth.

This book is about human evolution, and we will spend a lot of time explaining how natural selection and other evolutionary processes have shaped the human species. Before we begin, it is important to consider why you should care about this topic. Many of you will be working through this book as a requirement for an undergraduate class in biological anthropology and will read the book in order to earn a good grade. As instructors of a class like this ourselves, we approve of this motive. However, there is a much better reason to care about the processes that have shaped human evolution: understanding how humans evolved is the key to understanding why people look and behave the way they do.

The profound implications of evolution for our understanding of humankind were apparent to Darwin from the beginning. We know this today because he kept notebooks in which he recorded his private thoughts about various topics. The quotation that begins this prologue is from the *M Notebook*, begun in July 1838, in which Darwin jotted down his ideas about humans, psychology, and the philosophy of science. In the nineteenth century, metaphysics involved the study of the human mind. Thus Darwin was saying that because he believed humans evolved from a creature something like a baboon, it followed that an understanding of the mind of a baboon would contribute more to an understanding of the human mind than would all of the works of the great English philosopher John Locke.

Darwin's reasoning was simple. Every species on this planet has arisen through the same evolutionary processes. These processes determine why organisms are the way they are by shaping their morphology, physiology, and behavior. The traits that characterize the human species are the result of the same evolutionary processes that created all other species. If we understand these processes, and the conditions under which the human species evolved, then we will have the basis for a scientific understanding of human nature. Trying to comprehend the human mind without an understanding of human evolution is, as Darwin wrote in another notebook that October, "like puzzling at astronomy without mechanics." By this, Darwin meant that his theory of evolution could play the same role in biology and psychology that Isaac Newton's laws of motion had played in astronomy. For thousands of years, stargazers, priests, philosophers, and mathematicians had struggled to understand the motions of the planets without success. Then, in the late 1600s, Newton discovered the laws of mechanics and showed how all of the intricacies in the dance of the planets could be explained by the action of a few simple processes (Figure 3).

In the same way, understanding the processes of evolution enables us to account for the stunning sophistication of organic design and the diversity of life, and to understand why people are the way they are. As a consequence, understanding how natural selection and other evolutionary processes shaped the human species is relevant to all of the academic disciplines that are concerned with human beings. This vast intellectual domain includes medicine, psychology, the social sciences, and even the humanities. Beyond academia, understanding our own evolutionary history can help

FIGURE 1 When this portrait of Charles Darwin was painted, he was about 30 years old. He had just returned from his voyage on the HMS *Beagle* and was still busy organizing his notes, drawings, and vast collections of plants and animals.

FIGURE 2 Thomas Malthus was the author of *An Essay on the Principle of Population*, a book Charles Darwin read in 1838 that profoundly influenced the development of his theory of evolution by natural selection.

FIGURE 3 Sir Isaac Newton discovered the laws of celestial mechanics, a body of theory that resolved age-old mysteries about the movements of the planets.

us answer many questions that confront us in everyday life. Some of these questions are relatively trivial: Why do we sweat when hot or nervous? Why do we crave salt, sugar, and fat, even though large amounts of these substances cause disease (Figure 4)? Why are we better marathon runners than mountain climbers? Other questions are more profound: Why do only women nurse their babies? Why do we grow old and eventually die? Why do people look so different around the world? As you will see, evolutionary theory provides answers or insights about all of these questions. Aging, which eventually leads to death, is an evolved characteristic of humans and most other creatures. Understanding how natural selection shapes the life histories of organisms tells us why we are mortal, why our life span is about 70 years, and why other species live shorter lives. In an age of horrific ethnic conflicts and growing respect for multicultural diversity, we are constantly reminded of the variation within the human species. Evolutionary analyses tell us that genetic differences between human groups are relatively minor, and that our notions of race and ethnicity are culturally constructed categories, not biological realities.

All of these questions deal with the evolution of the human body. However, understanding evolution is also an important part of our understanding of human behavior and the human mind. The claim that understanding evolution will help us understand contemporary human behavior is much more controversial than the claim that it will help us understand how human bodies work. But it should not be. The human brain is an evolved organ of great complexity, just like the endocrine system, the nervous system, and all of the other components of the human body that regulate our behavior. Understanding evolution helps us understand our minds and behavior because evolutionary processes forged the brain that controls human behavior, just as they forged the brain of the chimpanzee and the salamander.

One of the great debates in Western thought centers on the essence of human nature. One view is that people are basically honest, generous, and cooperative creatures who are corrupted by an immoral economic and social order. The opposing view is that we are fundamentally amoral, egocentric beings whose antisocial impulses are held in check by social pressures. This question turns up everywhere. Some people believe that children are little barbarians who are civilized only through sustained parental effort; others think that children are gentle beings who are socialized into competitiveness and violence by exposure to negative influences like toy guns and violent TV programs (Figure 5). The same dichotomy underpins much political and economic thought. Economists believe that people are rational and selfish, but other social scientists, particularly anthropologists and sociologists, question and sometimes reject this assumption. We can raise an endless list of interesting questions about human nature: Does the fact that, in most societies, women rear children and men make war mean that men and women differ in their innate predispositions? Why do men typically find younger women attractive? Why do some people neglect and abuse their children, while others adopt and lovingly raise children who are not their own?

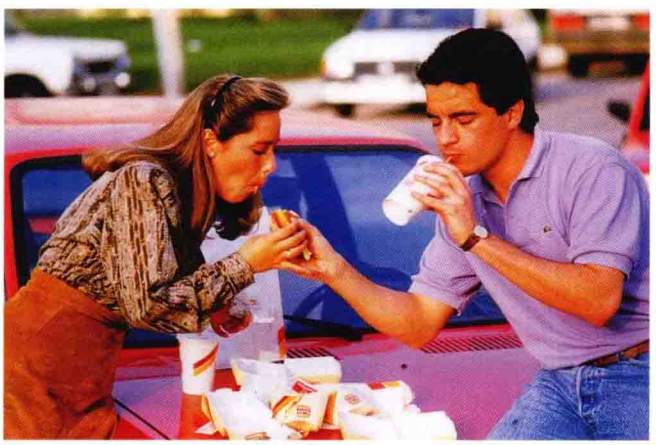

FIGURE 4 A strong appetite for sugar, fat, and salt may have been adaptive for our ancestors, who had little access to sweet, fatty, and salty foods. We have inherited these appetites and have easy access to these foods. As a consequence, many of us suffer from obesity, high blood pressure, diabetes, and heart disease.

Understanding human evolution does not reveal the answers to all of these questions, or even provide a complete answer to any one of them. As we will see, however, it can provide useful insights about all of them. An evolutionary

approach does not imply that behavior is "genetically determined," or that learning and culture are unimportant. In fact, we will argue that learning and culture play crucial roles in human behavior. Behavioral differences among peoples living in different times and places result mainly from flexible adjustments to different social and environmental conditions. Understanding evolution is useful precisely because it helps us understand why humans respond in different ways to different conditions.

FIGURE 5 One of the great debates in Western thought focuses on the essential elements of human nature. Are people basically moral beings corrupted by society, or fundamentally amoral creatures socialized by cultural conventions, social strictures, and religious beliefs?

OVERVIEW OF THE BOOK

Humans are the product of organic evolution. By this we mean that there is an unbroken chain of descent that connects every living human being to a bipedal, apelike creature that walked through tall grasses of the African savanna 3 million years ago (mya); to a monkeylike animal that clambered through the canopy of great tropical forests covering much of the world 35 mya; and finally to a small, egg-laying, insect-eating mammal that scurried about at night during the age of the dinosaurs, 100 mya. To understand what we are now, you have to understand how this transformation took place. We tell this story in four parts.

Part One: How Evolution Works

More than a century of hard work has given us a good understanding of how evolution works. The transformation of apes into humans involved the assembly of many new, complex adaptations. For example, in order for early humans to walk upright on two legs, there had to be coordinated changes in many parts of their bodies, including their feet, legs, pelvis, backbone, and inner ear. Understanding how natural selection gives rise to such complex structures, and why the genetic system plays a crucial role in this process, is essential for understanding how new species arise. An understanding of these processes also allows us to reconstruct the history of life from the characteristics of contemporary organisms.

Part Two: Primate Behavior and Ecology

In the second part of the book, we consider how evolution has shaped the behavior of nonhuman primates—an exercise that helps us understand human evolution in two ways. First, humans are members of the primate order: we are more similar to other primates, particularly the great apes, than we are to wolves, raccoons, or other mammals. Studying how primate morphology and behavior are affected by ecological conditions helps us determine what our ancestors might have been like and how they may have been transformed by natural selection. Second, we study primates because they are an extremely diverse order and are particularly variable in their social behavior. Some are solitary, others live in monogamous pairs, and some live in large groups that contain many adult females and males. Data derived from studies of these species help us understand how social behavior is molded by natural selection. We can then use these insights to interpret the hominin fossil record and the behavior of contemporary people (Figure 6).

FIGURE 6 We will draw on information about the behavior of living primates, such as this chimpanzee, to understand how behavior is molded by evolutionary processes, to interpret the hominin fossil record, and to draw insights about the behavior of contemporary humans.

FIGURE 7 Fossils painstakingly excavated from many sites in Africa, Europe, and Asia provide us with a record of our history as a species. Two million years ago in Africa, there were a number of apelike species that walked bipedally but still had ape-sized brains and apelike developmental patterns. These are the fossilized remains of *Australopithecus habilis*, a species that some think is ancestral to modern humans.

Part Three: The History of the Human Lineage

General theoretical principles are not sufficient to understand the history of any lineage, including our own. The transformation of a shrewlike creature into the human species involved many small steps, and each step was affected by specific environmental and biological circumstances. To understand human evolution, we have to reconstruct the actual history of the human lineage and the environmental context in which these events occurred. Much of this history is chronicled in the fossil record. These bits of mineralized bone, painstakingly collected and reassembled by paleontologists, document the sequence of organisms that link early mammals to modern humans. Complementary work by geologists, biologists, and archaeologists allows us to reconstruct the environments in which the human lineage evolved (Figure 7).

Part Four: Evolution and Modern Humans

Finally, we turn our attention to modern humans and ask why we are the way we are. Why is the human species so variable? How do we acquire our behavior? How has evolution shaped human psychology and behavior? How do we choose our mates? Why do people commit infanticide? Why have humans succeeded in inhabiting every corner of the Earth when other species have more limited ranges? We will explain how an understanding of evolutionary theory and a knowledge of human evolutionary history provide a basis for addressing questions like these.

The history of the human lineage is a great story, but it is not a simple one. The relevant knowledge is drawn from many disciplines in the natural sciences, such as physics, chemistry, biology, and geology; and from the social sciences, mainly anthropology, psychology, and economics. Learning this material is an ambitious task, but it offers a very satisfying reward. The better you understand the processes that have shaped human evolution and the historical events that took place in the human lineage, the better you will understand how we came to be and why we are the way we are.

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