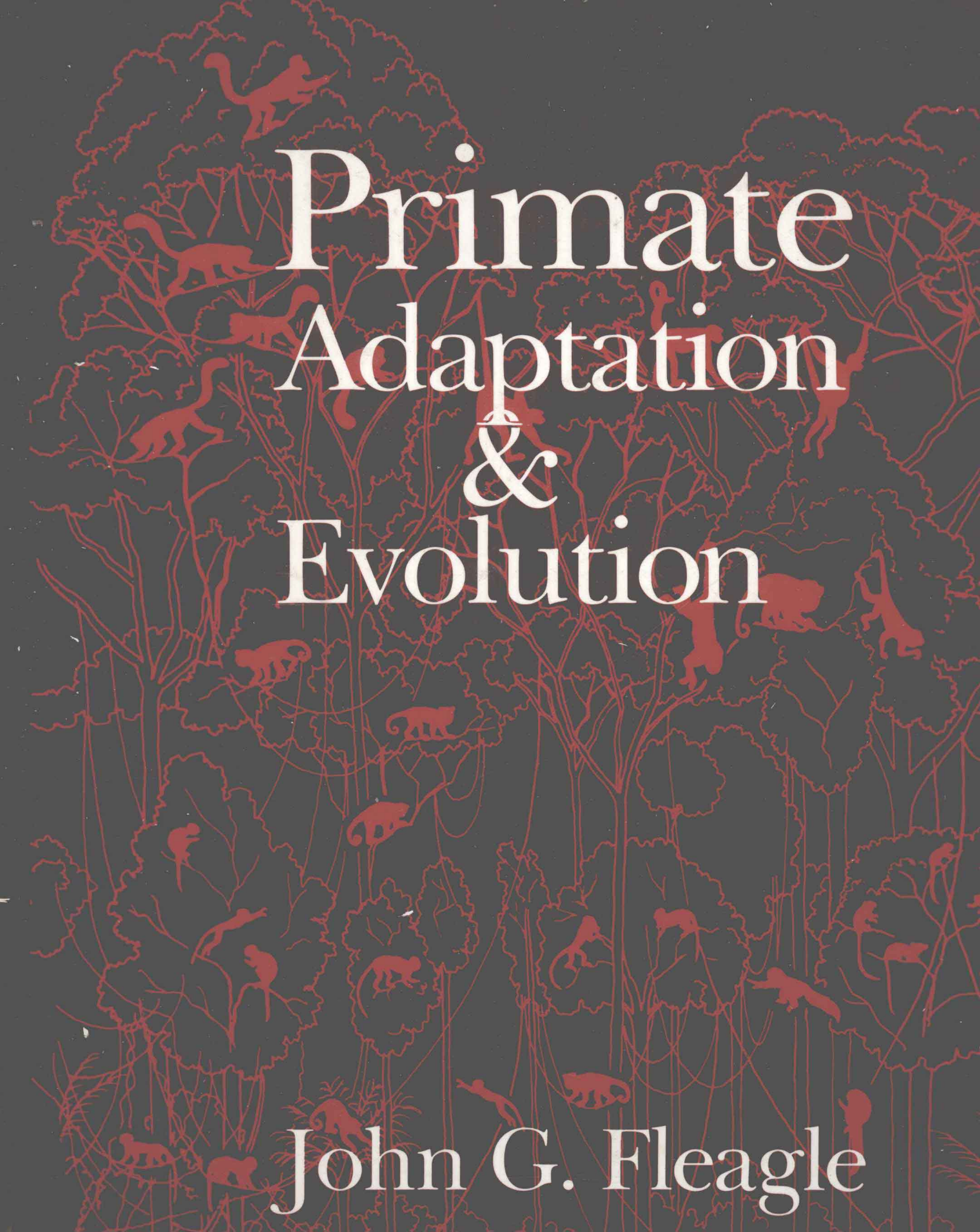

Primate Adaptation & Evolution

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TABLES & ILLUSTRATIONS

Tables

Illustrations

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 6

CHAPTER 7

CHAPTER 12

CHAPTER 13

CHAPTER 14

CHAPTER 15

CHAPTER 16

PREFACE

This book is an introduction to the biology of the mammalian order Primates. It is based on the contents of a course that has been offered to advanced undergraduate and beginning graduate students in anthropology and biology at the State University of New York at Stony Brook during the past ten years. It is designed for students with a general knowledge of basic biology and evolutionary theory who wish to examine the comparative anatomy, behavioral ecology, and paleontology of humans and their nearest relatives, a particularly well-studied and interesting group of animals. Anthropology textbooks beyond the freshman level have traditionally been devoted either to primate behavior and ecology or to primate and human evolution. This is unfortunate, since our understanding of the evolutionary history of primates hinges on our ability to interpret fossil bones and teeth from a comparison of these elements with those in the bodies of extant primates.

In this book, the major groups of living and extinct primates are presented as a series of adaptive radiations. For each radiation I examine those aspects of their biology that set them apart from other primates and those features they share with other members of the order. The book is divided into three sections. The first three chapters—references or primers on evolutionary biology, primate anatomy, and behavioral ecology—are designed to introduce the basic concepts and terminology used in later chapters. Chapters 4 through 7 cover the anatomy, ecology, and systematics of the major groups of extant primates—prosimians, New World monkeys, Old World monkeys, and hominoids. Each group is discussed genus by genus, with particular emphasis on diagnostic skeletal features and characteristic dietary and locomotor adaptations. Within each chapter are tables providing the species-level taxonomy of each group as well as common names, body weights, and limb proportions for each species. Each chapter includes more general discussions of the adaptive radiation of the group being considered as well as discussions of current issues concerning evolutionary relationships among the taxa. These chapters contain comparative anatomical drawings designed to illustrate the diagnostic features of each taxonomic group as well as summary charts reviewing the adaptive radiations. In addition, most genera are pictured in a series of drawings of animals in their natural environments which illustrate not only external appearance but also aspects of the typical habitat, diet, and locomotor and postural habits.

In Chapter 8, "Primate Adaptations," I examine common adaptive patterns in morphology and behavior that can be traced throughout the order Primates. This review provides a summary of adaptive themes from earlier chapters as well as a basis for interpretation of the adaptations of fossil taxa in later chapters.

In the remainder of the book, Chapters 9 through 16, we are concerned with the primate fossil record. Chapter 9, an introduction to paleontology, reviews the major differences between our knowledge of fossil primates and our understanding of living species. Chapters 10 through 15 are analyses of the fossil records of particular radiations of primates, beginning with the plesiadapiforms of the Paleocene and continuing through the evolution of hominids in the Pliocene and Pleistocene. As in the earlier chapters on living species, each radiation is considered in terms of its distinctive morphological characteristics and its adaptive diversity. Tables provide more detailed, species-level systematics, with estimated body weights based on regressions of dental dimensions to give the reader a comparative scale for visualizing the extinct primates. As in the chapters of living primates, there are discussions of the adaptive diversity of various extinct radiations as well as sections outlining current issues and unresolved problems on the evolutionary relationships of each group. In the final chapter, I survey 65 million years of primate evolution for evidence of general patterns in adaptive diversity and evolutionary mechanisms.

Although the book is designed as a single treatment of living and fossil primates, the arrangement is suitable for use in a less comprehensive course in either primate ecology or primate evolution. In addition, it should provide an introduction to primatology for biologists of all sorts.

This book has been many years in the making, and I have relied heavily on the good will and expertise of many colleagues and friends. The students of primate evolution at Stony Brook prompted me to write down my notes and provided me with numerous comments on early drafts of most chapters, as did students at the University of California, Berkeley, where I had the pleasure of teaching in 1986. Much of the material in these chapters is the result of interaction with my longtime friends and colleagues Russell Mittermeier, David Chivers, Elwyn Simons, Ken Rose, Phil Gingerich, Tom Bown, and especially Richard Kay. For the past thirteen years I have had the opportunity to work in the Department of Anatomical Sciences at Stony Brook with Gabor Inke, Jack Stern, Norman Creel, William Jungers, Randall Susman, David Krause, Sue Larson, Russell Mittermeier, Fred Grine, Lawrence Martin, and for all too brief a time Alfred Rosenberger and James Wells—a group of the most outstanding (and outrageous) primatologists ever assembled in one university. We owe a special debt to our chairman, Maynard Dewey, whose support has made this a truly enjoyable and productive place to work.

Much of the delight in putting together this book has come from the opportunity to work with several outstanding artists. Stephen Nash, Hugh Nachamie, Luci Betti, and Leslie Jungers all contributed greatly to the illustrations in this book, Jeff Meldrum helped with several maps and charts, and J. Muennig provided photographs. Many people and institutions generously provided copies of illustrations for use in the book, including Tom Bown, Eric Delson, Richard Kay, Gerald Eck, Ken Rose, Elwyn Simons, Leonard Ginsburg, Phil Gingerich, Brian Shea, W. von Koenigswald, Ronald Wolff, Kathy Schick, Jeanne Sept, Gunter Bräuer, Fred Grine, Vince Sarich, David Pilbeam, Tim White, B. Holly Smith, Russell Mittermeier, Meave Leakey, Russell Ciochon, Peter Andrews, Lawrence Martin, Wolfgang Maier, Mary Maas, Pan Yuerong, the Institute of Human Origins, and the National Museums of Kenya. Stephanie Rippel, Nancy Thompson Handler, and Mary Maas were invaluable in helping me go through many drafts of the text, sort out the bibliographies, and complete the index.

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CONTENTS

SIX
Old World Monkeys

SEVEN
Apes and Humans

EIGHT
Primate Adaptations

NINE
The Fossil Record

TEN
Archaic Primates

ELEVEN
Fossil Prosimians

TWELVE
Early Anthropoids and Fossil Platyrrhines

ONE

Adaptation, Evolution, and Systematics

ORDER PRIMATES

The subject of this book is the order Primates, the mammalian order that includes not only us humans but also a wide array of lemurs, lorises, galagos, tarsiers, monkeys, and apes. It also includes many extinct animals that are known to us only through fossilized remains and lack familiar names. Primates come in a variety of sizes and shapes, and this variety is matched by the diversity of behaviors primates have evolved to survive in equally various environments. This diversity in structure and behavior—and its evolution—is the theme of this book. Before considering this diversity, we review a few principles of evolutionary biology and discuss the mechanisms through which this array of creatures has come about. We also provide a brief review of biological classification and methods of reconstructing phylogeny.

Adaptation

Adaptation is a concept central to our understanding of evolution, but the term has proved very difficult to define in a simple phrase. One of the most succinct definitions has been offered by Vermeij (1978, p. 3): "An *adaptation* is a characteristic that allows an organism to live and reproduce in an environment where it probably could not otherwise exist." In the following chapters, we examine extant (living) and extinct (fossil) primates as a series of **adaptive radiations**—groups of closely related organisms that have evolved morphological and behavioral features enabling them to exploit different ecological niches. Adaptive radiations are central to our understanding of evolutionary processes. The adaptive radiation of finches on the Galapagos Islands of Ecuador played an important role in guiding Darwin's views on the origin of species.

"Adaptation" also refers to the process whereby organisms obtain their adaptive characteristics. The primary mechanism of adaptation is **natural selection**—the differential survival and reproductive success of individuals with different heritable characteristics. As Darwin argued, and subsequent generations of scientists have corroborated, natural selection ensures that any heritable features, either anatomical or behavioral, that increase the fitness of an individual relative to other individuals will be passed on to succeeding generations. In considering the evolution of behavioral traits in the following chapters, it is important to remember that natural selection acts primarily