



# Primate Adaptation & Evolution

John G. Fleagle

---

# Primate Adaptation & Evolution

---

John G. Fleagle

State University of New York, Stony Brook



ACADEMIC PRESS

Harcourt Brace and Company

San Diego New York Boston London Sydney Tokyo Toronto

---

Copyright © 1988 by Academic Press  
All Rights Reserved.

No part of this publication may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopy, recording or any information storage and retrieval system, without permission in writing from the publisher.

ACADEMIC PRESS  
525 B Street, Suite 1900  
San Diego, California 92101-4495

*United Kingdom Edition published by*  
ACADEMIC PRESS LIMITED  
24-28 Oval Road, London NW1 7DX

**Library of Congress Cataloging-in-Publication Data**

Fleagle, John G.

Primate adaptation and evolution.

Includes index.

1. Primates—Evolution. 2. Adaptation (Biology)

I. Title.

QL737.P9F57 1988 599'.0438 87-6508

ISBN 0-12-260340-0

PRINTED IN THE UNITED STATES OF AMERICA

97 EB 9 8 7 6 5

---

## Tables

- 1.1 A classification of the tufted capuchin monkey 5
- 2.1 Skeletal proportions 34

### EXTANT AND SUBFOSSIL PRIMATES

- 4.1 Family Cheirogaleidae 73
- 4.2 Family Lemuridae 77
- 4.3 Family Lepilemuridae 81
- 4.4 Family Indridae 83
- 4.5 Family Daubentonidae 87
- 4.6 Family Galagidae 95
- 4.7 Family Lorisidae 97
- 4.8 Family Tarsiidae 101
- 5.1 Subfamily Pitheciinae 120
- 5.2 Subfamily Aotinae 125
- 5.3 Subfamily Cebinae 127
- 5.4 Subfamily Atelinae 130
- 5.5 Subfamily Callitrichinae 137
- 6.1 Family Cercopithecidae, Subfamily Cercopithecinae, macaques 165
- 6.2 Family Cercopithecidae, Subfamily Cercopithecinae, mangabeys 168
- 6.3 Family Cercopithecidae, Subfamily Cercopithecinae, baboons 169
- 6.4 Family Cercopithecidae, Subfamily Cercopithecinae, guenons 173
- 6.5 Family Cercopithecidae, Subfamily Colobinae, colobus monkeys 180
- 6.6 Family Cercopithecidae, Subfamily Colobinae, langurs 183
- 6.7 Family Cercopithecidae, Subfamily Colobinae, odd-nosed monkeys 190
- 7.1 Family Hylobatidae 205
- 7.2 Family Pongidae 211
- 7.3 Family Hominidae 221

### FOSSIL PRIMATES

- 10.1 *Purgatorius* 271
- 10.2 Family Microsyopidae 275
- 10.3 Family Plesiadapidae 279
- 10.4 Family Carpolestidae 280
- 10.5 Family Saxonellidae 281
- 10.6 Family Paromomyidae 281
- 10.7 Family Picrodontidae 283
- 11.1 Family Adapidae, Subfamily Notharctinae 294
- 11.2 Family Adapidae, Subfamily Adapinae 297
- 11.3 Family Adapidae, Subfamily Sivaladapinae 303
- 11.4 Family Adapidae, Subfamily *incertae sedis* 303
- 11.5 Superfamily Lorisioidea 304
- 11.6 Family Omomyidae, Subfamily Anaptomorphinae 308
- 11.7 Family Omomyidae, Subfamily Omomyinae 310
- 11.8 Family Omomyidae, Subfamily Microchoerinae 311
- 11.9 Family Omomyidae, Asian omomyids 313
- 11.10 Family Tarsiidae 313
- 12.1 Possible earliest anthropoids 326
- 12.2 Family Parapithecidae 331
- 12.3 Superfamily Hominoidea 336
- 12.4 Infraorder Platyrrhini 344
- 13.1 Early and middle Miocene apes 365
- 13.2 Family Pliopithecidae 376
- 13.3 Family Oreopithecidae 380
- 13.4 Family Pongidae 382
- 14.1 Family Victoriapithecidae, Subfamily Victoriapithecinae 399

- 14.2 Family Cercopithecidae, Subfamily  
Cercopithecinae 402
- 14.3 Family Cercopithecidae, Subfamily  
Colobinae 405
- 15.1 Family Hominidae 417

## Illustrations

### CHAPTER 1

- 1.1 Shared specializations and ancestral  
features 3
- 1.2 A primate classification 6
- 1.3 Two approaches to ape and human  
classification 8

### CHAPTER 2

- 2.1 Mouse lemur and gorilla, the smallest and  
largest living primates 12
- 2.2 Primate size ranges 13
- 2.3 A human skull 13
- 2.4 Skulls of a capuchin and a lemur 14
- 2.5 Siamang dentition 16
- 2.6 Primitive primate dentition 17
- 2.7 Primate skull and chewing muscles 18
- 2.8 Primate muscles of facial expression 18
- 2.9 Primate brains 19
- 2.10 Functional areas of the human brain 21
- 2.11 Primate cranial blood supply 22
- 2.12 Primate nasal regions 23
- 2.13 Mammal and primate eye orbits 24
- 2.14 A primate ear 25
- 2.15 Primate tympanic structures 26
- 2.16 Spider monkey skeleton 27
- 2.17 Baboon skeleton and limb  
musculature 28
- 2.18 Terminology for anatomical  
orientation 29
- 2.19 Skeleton of a baboon hand 30
- 2.20 Hand skeleton and palm of six  
primates 31
- 2.21 Skeleton of a baboon foot 33
- 2.22 Foot skeleton and foot of six primates 34
- 2.23 Orangutan digestive system 35
- 2.24 Gorilla reproductive organs 37
- 2.25 Fetal membranes in three primates 38
- 2.26 Primate and nonprimate mammal growth  
curves 39

- 2.27 Primate life history parameters 40
- 2.28 Primate dental eruption sequences 41

### CHAPTER 3

- 3.1 Primate geographic distribution 46
- 3.2 Primate habitats 47
- 3.3 Rain forest microhabitats 48
- 3.4 Primate land use 50
- 3.5 Benefits and costs of diurnality and  
nocturnality 52
- 3.6 Primate activity histograms 53
- 3.7 Primate locomotor behaviors 55
- 3.8 Primate feeding postures 56
- 3.9 Primate social groups 57

### CHAPTER 4

- 4.1 Geographic distribution of extant  
prosimians 67
- 4.2 Gradistic and phyletic classifications of  
primates 68
- 4.3 Malagasy strepsirrhine dentitions 69
- 4.4 Distinctive strepsirrhine skeletal  
features 70
- 4.5 Strepsirrhine skulls 70
- 4.6 Forest types in Madagascar 71
- 4.7 Five cheirogaleid genera 72
- 4.8 Diet and forest height preference for five  
sympatric Malagasy prosimians 73
- 4.9 Brown lemur, ruffed lemur, and ring-  
tailed lemur 76
- 4.10 Gentle lemur 79
- 4.11 Sportive lemur 80
- 4.12 Sifaka, indris, and woolly lemur 82
- 4.13 Indriid skulls 84
- 4.14 Indris skeleton 85
- 4.15 Aye-aye 86
- 4.16 Reconstructed Malagasy natural setting,  
ca. 8,000–1,000 B.P., with typical subfossil  
prosimians 88
- 4.17 *Palaeopropithecus ingens* skeleton 89
- 4.18 Adaptive diversity of the Malagasy  
prosimians 91
- 4.19 Sympatric galagos and lorises from  
Gabon 93
- 4.20 Diet and forest height preference for five  
sympatric galagos and lorises from  
Gabon 94
- 4.21 Slow loris and slender loris 98

- 4.22 A strepsirhine phylogeny 99
- 4.23 Biomolecular phylogenies of the strepsirhines 99
- 4.24 Skull, dentition, and skeleton of *Tarsius* 101
- 4.25 Tarsier 102

**CHAPTER 5**

- 5.1 Characteristic anatomical features of anthropoids and prosimians 113
- 5.2 Geographic distribution of extant and extinct platyrrhines 114
- 5.3 Platyrrhine and catarrhine characteristics 115
- 5.4 Platyrrhine dentitions adapted to different diets 115
- 5.5 Platyrrhine skulls 116
- 5.6 Sympatric platyrrhines from Surinam 117
- 5.7 Diet and forest height preference for seven sympatric platyrrhines from Surinam 118
- 5.8 Bearded saki and white-faced saki 121
- 5.9 Bearded saki skeleton 122
- 5.10 Nuts in the bearded saki diet 123
- 5.11 Owl monkey 124
- 5.12 Tufted capuchin and squirrel monkey 126
- 5.13 Squirrel monkey skeleton 128
- 5.14 Red howling monkey 131
- 5.15 Woolly monkey 133
- 5.16 Black spider monkey 134
- 5.17 Woolly spider monkey 136
- 5.18 Unusual features of callitrichines 138
- 5.19 Goeldi's monkey 139
- 5.20 Tamarin faces 140
- 5.21 White-lipped tamarin and saddle-back tamarin 141
- 5.22 Golden lion tamarin 143
- 5.23 Tamarin and marmoset dentition 145
- 5.24 Marmoset faces 145
- 5.25 Pygmy marmoset 146
- 5.26 Adaptive diversity of the platyrrhines 147
- 5.27 Platyrrhine phylogenies based on teeth, skulls, and skeletons 149
- 5.28 A biomolecular platyrrhine phylogeny 150

**CHAPTER 6**

- 6.1 Characteristic anatomical features of cercopithecoids and hominoids 160
- 6.2 Geographic distribution of extant cercopithecoid monkeys 161
- 6.3 Characteristic features of colobines and cercopithecines 162
- 6.4 Skulls of cercopithecines and colobines 163
- 6.5 Crab-eating macaque and pig-tailed macaque 164
- 6.6 Diet, forest height preference, and locomotor behavior of six sympatric catarrhines from Malaysia 167
- 6.7 Savannah baboon 169
- 6.8 Baboon skeleton 170
- 6.9 Gelada 172
- 6.10 Guenon faces 174
- 6.11 Crowned guenon, spot-nosed guenon, and moustached monkey 175
- 6.12 Diet and forest height preference of five monkeys from Gabon 176
- 6.13 De Brazza's monkey 177
- 6.14 Vervet monkey 178
- 6.15 Red colobus and black-and-white colobus 181
- 6.16 Purple-faced monkey and Hanuman langur 185
- 6.17 Spectacled langur and banded leaf monkey 186
- 6.18 Locomotor and anatomical differences between *Presbytis melalophos* and *Presbytis obscura* 188
- 6.19 Proboscis monkey 189
- 6.20 Golden monkey 191
- 6.21 Adaptive diversity of Old World monkeys 192
- 6.22 Morphological and biomolecular phylogenies of Old World monkeys 193

**CHAPTER 7**

- 7.1 Geographic distribution of extant apes 203
- 7.2 Characteristic skeletal features of extant apes 204
- 7.3 Geographic distribution and facial characteristics of extant gibbons 206

- 7.4 Siamang and orangutan lower jaws 207
- 7.5 Gibbon skeleton 207
- 7.6 White-handed gibbon and siamang 208
- 7.7 Locomotor behavior and feeding postures of the Malayan siamang 210
- 7.8 Orangutan 212
- 7.9 Mountain gorilla 214
- 7.10 Gorilla skeleton 215
- 7.11 Common chimpanzee 217
- 7.12 Bonobo 218
- 7.13 The cranial allometry of African apes, with skull sizes and shapes 220
- 7.14 Human 221
- 7.15 Human skeleton 221
- 7.16 Adaptive radiation of living hominoids 223
- 7.17 Phyletic relationships among hominoids 224

**CHAPTER 8**

- 8.1 Mathematical relations between linear, areal, and volumetric dimensions 232
- 8.2 Femora of a gorilla and a pygmy marmoset 233
- 8.3 Growth allometry, intraspecific allometry, and interspecific allometry 234
- 8.4 Correlation of primate body size and diet 235
- 8.5 Correlation of primate body size and locomotor behavior 237
- 8.6 Locomotor consequences of body size 237
- 8.7 Postural consequences of body size 238
- 8.8 Correlation of primate body size and home range size 239
- 8.9 Primate anatomical adaptations to diet 240
- 8.10 Anatomical features associated with primate arboreal quadrupedalism 245
- 8.11 Anatomical features associated with primate terrestrial quadrupedalism 247
- 8.12 Anatomical features associated with primate leaping 248
- 8.13 Anatomical features associated with primate suspensory behavior 249
- 8.14 Anatomical features associated with human bipedalism 251

- 8.15 Canine differences between monogamous gibbons and polygynous baboons 254
- 8.16 Morphological features associated with differences in social organization 254

**CHAPTER 9**

- 9.1 A geological time scale for the Cenozoic era 259
- 9.2 Positions of the continents during the past 180 million years 260
- 9.3 Temperatures and sea levels during the Cenozoic era 261
- 9.4 Types of fossils 262
- 9.5 The history of a fossil 263

**CHAPTER 10**

- 10.1 The middle Paleocene world and archaic primate fossil sites 269
- 10.2 Reconstructed North American late Paleocene setting, with typical plesiadapiforms 272
- 10.3 Abundance of different mammalian orders in a late Paleocene fossil site in western North America 273
- 10.4 Plesiadapiform mandibles 273
- 10.5 Plesiadapiform skulls 274
- 10.6 Anterior dentitions of plesiadapiforms compared to those of a marsupial and a hedgehog 276
- 10.7 A plesiadapid phylogeny, showing dental and cranial diversity and probable dietary associations 278
- 10.8 Premolar shape in three carpolestid genera 280
- 10.9 The phyletic position of plesiadapiforms 284

**CHAPTER 11**

- 11.1 Geographic distribution of fossil prosimian sites 289
- 11.2 Anatomical differences between fossil prosimians and archaic plesiadapiforms 291
- 11.3 Adapid mandibles 292
- 11.4 Reconstructed skulls of *Smilodectes* and *Adapis* 293



- 
- |   |  |
|---|--|
| <p>11.5 Reconstructed skeleton of <i>Smilodectes gracilis</i> 293</p> <p>11.6 Phylogeny of notharctines from northern Wyoming 295</p> <p>11.7 Phylogeny of European adapines 298</p> <p>11.8 Lower dentitions of <i>Adapis parisiensis</i> and <i>Hapalemur griseus</i> 299</p> <p>11.9 Reconstructed late Eocene setting in the Paris Basin, showing typical primates 300</p> <p>11.10 Hindlimb of a fossil adapine from Messel, Germany 301</p> <p>11.11 <i>Sivaladapis nagrii</i> dentition 302</p> <p>11.12 Skull of <i>Mioeuoticus</i> 305</p> <p>11.13 Lower jaw of <i>Teilhardina americana</i> 306</p> <p>11.14 Omomyid mandibles 306</p> <p>11.15 Cranial morphology of adapids and omomyids 307</p> <p>11.16 Omomyid skulls compared to those of living nocturnal primates 307</p> <p>11.17 Omomyid dentitions, showing dietary adaptations 309</p> <p>11.18 Dentition of <i>Necrolemur antiquus</i> compared to that of <i>Tarsius syrichta</i> 312</p> <p>11.19 Fossil tarsiid lower molars 314</p> <p>11.20 Body size of North American adapids, anaptomorphine omomyids, and omomyine omomyids through time 316</p> <p>11.21 Body size of European adapids and microchoerine omomyids through time 317</p> <p>11.22 Phyletic relationships of adapids and omomyids 319</p> <p><b>CHAPTER 12</b></p> <p>12.1 Geographic distribution of early fossil anthropoids and platyrrhines 325</p> <p>12.2 <i>Amphipithecus</i> and <i>Pondaungia</i> 326</p> <p>12.3 The Fayum Depression 327</p> <p>12.4 Stratigraphic section of the Jebel Qatrani Formation, Fayum, Egypt 328</p> <p>12.5 Reconstruction of the early Oligocene Fayum environment 329</p> <p>12.6 Reconstruction of <i>Aegyptopithecus zeuxis</i>, <i>Propithecus chirobates</i>, and <i>Apidium phiomense</i> 330</p> <p>12.7 Parapithecoid lower dentitions 331</p> <p>12.8 Reconstructed facial skeleton of <i>Apidium phiomense</i> 332</p> | <p>12.9 Restored skeleton of <i>Apidium phiomense</i> 333</p> <p>12.10 The phyletic position of parapithecoids 335</p> <p>12.11 <i>Propithecus chirobates</i> mandible 336</p> <p>12.12 Cranial remains of <i>Aegyptopithecus zeuxis</i> 337</p> <p>12.13 Reconstructed skeleton of <i>Aegyptopithecus zeuxis</i> 338</p> <p>12.14 The phyletic relationships of <i>Aegyptopithecus</i> and <i>Propithecus</i> to later catarrhines 339</p> <p>12.15 Jaw of <i>Oligopithecus savagei</i> 340</p> <p>12.16 Adaptive characteristics of early Oligocene Fayum anthropoids compared to those of extant platyrrhines and catarrhines and early Miocene catarrhines 341</p> <p>12.17 Phyletic position of early Fayum anthropoids 342</p> <p>12.18 A map of the neotropics, showing primate fossil localities 343</p> <p>12.19 Dental remains of <i>Branisella boliviana</i> 345</p> <p>12.20 Reconstructed skulls of <i>Tremacebus harringtoni</i> and <i>Dolichocebus gaimanensis</i> 345</p> <p>12.21 Mandible and lower dentition of <i>Soriacebus ameghinorum</i> 347</p> <p>12.22 Middle Miocene fossil primates from La Venta, Colombia 348</p> <p>12.23 A platyrrhine phylogeny, with fossil genera 350</p> <p>12.24 How did the ancestral platyrrhines reach South America? 351</p> <p>12.25 The South Atlantic in the Oligocene 352</p> <p><b>CHAPTER 13</b></p> <p>13.1 The early Miocene world and fossil ape locations 364</p> <p>13.2 East African early Miocene fossil localities 364</p> <p>13.3 Upper dentitions of early Miocene fossil apes 366</p> <p>13.4 Lower dentitions of early Miocene fossil apes 367</p> <p>13.5 Reconstructed faces of early Miocene fossil apes 367</p> <p>13.6 Reconstructed skulls of early Miocene fossil apes 368</p> |
|---|--|



- 
- |   |  |
|---|--|
| <p>13.7 Reconstructed skeleton of <i>Proconsul africanus</i> 369</p> <p>13.8 Reconstructed Kenyan early Miocene setting, with typical fossil apes 370</p> <p>13.9 Adaptive diversity of early Miocene apes 373</p> <p>13.10 Phyletic relationships of Oligocene and Miocene fossil catarrhines 375</p> <p>13.11 Cranial and dental remains of <i>Pliopithecus vindobonensis</i> 377</p> <p>13.12 Skeleton of <i>Pliopithecus</i> 378</p> <p>13.13 Cranial and dental remains of <i>Laccopithecus robustus</i> 379</p> <p>13.14 Dentition of <i>Oreopithecus bambolii</i> 381</p> <p>13.15 Skeleton of <i>Oreopithecus</i> 381</p> <p>13.16 Dental remains of <i>Dryopithecus</i> and <i>Sivapithecus</i> 383</p> <p>13.17 Cranial remains of <i>Sivapithecus</i> compared with <i>Pan</i> and <i>Pongo</i> 383</p> <p>13.18 Male and female lower jaws of <i>Graecopithecus macedoniensis</i> 384</p> <p>13.19 Lower jaws of <i>Gigantopithecus</i> and <i>Sivapithecus</i> compared with that of <i>Gorilla</i> 385</p> <p>13.20 Reconstruction of <i>Gigantopithecus</i> 386</p> <p>13.21 Changes in molar enamel thickness and rates of enamel deposition in fossil and extant apes 388</p> <p>13.22 Phyletic relationships of Miocene apes 389</p> <p><b>CHAPTER 14</b></p> <p>14.1 The modern Old World, with fossil monkey localities from the Miocene, Pliocene, and Pleistocene 398</p> <p>14.2 Lower jaws of <i>Prohylobates</i> and <i>Victoriapithecus</i> 399</p> <p>14.3 Dental and mandibular features of Oligocene anthropoids, early cercopithecoids, and modern cercopithecoids 400</p> <p>14.4 Skulls of <i>Theropithecus brumpti</i> and <i>Theropithecus gelada</i> 404</p> <p>14.5 Skeleton of <i>Theropithecus oswaldi</i> 405</p> <p>14.6 Skeleton of <i>Mesopithecus</i> 406</p> <p>14.7 Skull of <i>Libypithecus markgrafi</i> 407</p> | <p>14.8 Skulls of Plio-Pleistocene colobines compared with that of <i>Colobus polykomos</i> 408</p> <p>14.9 Cladogram of living and fossil Old World monkeys 409</p> <p>14.10 Relative species diversity of hominoids and cercopithecoids during the past 20 million years in Africa 410</p> <p><b>CHAPTER 15</b></p> <p>15.1 Fossil localities of <i>Australopithecus</i>, <i>Homo habilis</i>, and <i>Homo erectus</i> 415</p> <p>15.2 Geographic and temporal placement of early hominid sites in East Africa 416</p> <p>15.3 Skeleton of <i>Australopithecus afarensis</i>, "Lucy" 417</p> <p>15.4 Hominid footprints from Laetoli, Tanzania, ca. 3.5 million years B.P. 418</p> <p>15.5 Skeletons of <i>Australopithecus afarensis</i>, <i>Pan troglodytes</i>, and <i>Homo sapiens</i> 419</p> <p>15.6 A group of <i>Australopithecus afarensis</i> 420</p> <p>15.7 A group of <i>Australopithecus robustus</i> 423</p> <p>15.8 Cranial and dental features of <i>Australopithecus africanus</i> and <i>Australopithecus robustus</i> 424</p> <p>15.9 Differences in dental wear between <i>Australopithecus africanus</i> and <i>Australopithecus robustus</i> 425</p> <p>15.10 Dental development in <i>Australopithecus africanus</i>, <i>Homo habilis</i>, and contemporary humans and African apes 428</p> <p>15.11 Chronology of appearance of anatomical and behavioral features of East African hominids 430</p> <p>15.12 Theories of hominid bipedalism 431</p> <p>15.13 A hominid phylogeny 434</p> <p>15.14 Cranial and dental characteristics of <i>Homo habilis</i> and <i>Homo erectus</i> 436</p> <p>15.15 Primitive Oldowan tools 437</p> <p>15.16 Skeleton of <i>Homo erectus</i>, ca. 1.6 million years B.P. 439</p> <p>15.17 Cranial features of <i>Homo erectus</i>, Neandertals, and modern <i>Homo sapiens</i> 440</p> <p>15.18 A temporal placement of human cranial remains from Africa and Europe 442</p> |
|---|--|

**CHAPTER 16**

- |  |  |
|--|--|
| <p>16.1 Body size distribution of prosimians and Old World anthropoids through time 450</p> <p>16.2 Changes in dietary diversity of Old World higher primates 452</p> <p>16.3 Changes in substrate use of Old World higher primates 452</p> <p>16.4 Changes in arboreal locomotor habits of Old World higher primates 453</p> <p>16.5 Changes in taxonomic abundance of Old World higher primates 454</p> <p>16.6 The major primate radiations of the Cenozoic era 455</p> | <p>16.7 Speciation: changes in dentition of a lineage of early Eocene prosimians 457</p> <p>16.8 Speciation: changes in dentition of a lineage of early Eocene omomyids 458</p> <p>16.9 Cenozoic temperatures and major events in the primate fossil record of the Northern Hemisphere 460</p> <p>16.10 Competition and extinction: abundance of plesiadapiforms in the Paleocene and Eocene fossil record of North America compared with the abundance of early rodents and fossil prosimians 461</p> <p>16.11 Primates in danger of extinction 462</p> |
|--|--|

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.

Many people have provided helpful comments on one or more chapters over the past four years, including Russell Ciochon, Susan Larson, David Krause, Ken Rose, Elizabeth Watts, Charles Janson, Frances White, Steve Redhead, Roderick Moore, F. Clark Howell, Nancy Handler, Todd Olson, Marc Godinot, Chris Beard, Tom Naimen, Tim Cole, Elizabeth Dumont, Greg

Buckley, Liza Shapiro, Fred Grine, Mary Maas, and Randall Susman. William Jungers and Suzanne Strait provided both comments on the manuscript and invaluable assistance in compiling the tables of body weights. At Academic Press, Kerry Pinchbeck and John Thomas helped turn a ragged manuscript into a book. I am grateful for all their time, patience, and good humor. Finally, I owe extra thanks to Richard Kay, Lawrence Martin, and especially Patricia Wright, who contributed far more assistance with this book than one should normally expect from any colleague. I thank all of these people for their help and encouragement.

*Tables & Illustrations* ix  
*Preface* xvii

ONE

**Adaptation, Evolution,  
and Systematics**

Adaptation 1  
Evolution 2  
Phylogeny 2  
    Morphology • Biomolecular Phylogeny  
Taxonomy and Systematics 5  
Bibliography 9

TWO

**The Primate Body**

Size 11  
Cranial Anatomy 12  
    Bones of the Skull • Teeth and  
    Chewing • Muscles of Facial Expression  
The Brain and Senses 19  
    The Brain • Cranial Blood Supply •  
    Olfaction • Vision • Hearing  
The Trunk and Limbs 27  
    Axial Skeleton • Upper Limb •  
    Lower Limb • Limb Proportions  
Soft Tissues 35  
    Digestive System • Reproductive System  
Growth, Development, and Aging 39  
Bibliography 42

THREE

**Primate Life**

Primate Habitats 45  
    Forest Habitats • Habitats within the Forest •  
    Primates in Tropical Ecosystems  
Land Use 51  
Activity Patterns 51

A Primate Day 53  
Primate Diets 54  
Locomotion 54  
Social Life 57  
Why Primates Live in Groups 59  
    Improved Access to Food • Protection from  
    Predators • Access to Mates • Assistance in  
    Rearing Offspring  
Primate Communities 63  
Bibliography 63

FOUR

**Prosimians**

Malagasy Strepsirhines 68  
    Cheirogaleids • Lemurids • Lepilemurids •  
    Indriids • Daubentoniids  
Subfossil Malagasy Prosimians 87  
    Subfossil Indriids • Subfossil  
    Lemurids • Subfossil Lepilemurids  
Adaptive Radiation of Malagasy Primates 91  
Galagos and Lorises 92  
    Galagids • Lorises  
Adaptive Radiation of Galagos and Lorises 97  
Phyletic Relationships of Strepsirhines 98  
Tarsiers 100  
Phyletic Relationships of Tarsiers 103  
Bibliography 103

FIVE

**New World Anthropoids**

Anatomy of Higher Primates 112  
Platyrrhines 114  
    Pitheciines • Aotines • Cebines •  
    Atelines • Callitrichines  
Adaptive Radiation of Platyrrhines 147  
Phyletic Relationships of Platyrrhines 148  
Bibliography 150

## SIX

**Old World Monkeys**

- Catarrhine Anatomy 159
- Cercopithecoids 161
  - Cercopithecines • Colobines
- Adaptive Radiation of Old World Monkeys 191
- Phyletic Relationships of Old World Monkeys 192
- Bibliography 193

## SEVEN

**Apes and Humans**

- Hominoids 204
  - Hylobatids • Pongids • Size and Evolution of the African Apes • Hominids
- Adaptive Radiation of Hominoids 223
- Phyletic Relationships of Hominoids 224
- Bibliography 225

## EIGHT

**Primate Adaptations**

- Effects of Size 231
  - Size and Diet • Size and Locomotion • Size and Reproduction • Size and Ecology
- Adaptations to Diet 241
  - Dental Adaptations • Digestive Tract Adaptations • Diet and Ranging • Diet and Social Groups
- Locomotor Adaptations 244
  - Arboreal Quadrupeds • Terrestrial Quadrupeds • Leapers • Suspensory Primates • Bipeds • Locomotor Compromises • Locomotion and Ecology
- Anatomical Correlates of Social Organization 253
- Bibliography 255

## NINE

**The Fossil Record**

- Geological Time 258
  - Paleomagnetism • Continental Drift • Paleoclimate
- Fossils and Fossilization 261
- Paleoenvironments 264

- Reconstructing Behavior 265
- Paleobiogeography 265
- Bibliography 266

## TEN

**Archaic Primates**

- Primate Origins: *Purgatorius* 270
- Plesiadapiforms 271
  - Microsyopids • Plesiadapids • Carpolestids • Saxonellids • Paromomyids • Picrodontids
- Adaptive Radiation of Plesiadapiforms 283
- Plesiadapiforms and Later Primates 284
- Bibliography 285

## ELEVEN

**Fossil Prosimians**

- The First Modern Primates 290
- Adapids 292
  - Notharctines • Adapines • Sivaladapines • Possible African Adapids
- Are Adapids Strepsirrhines? 303
- Fossil Lorises and Galagos 304
- Omomyids 305
  - Anaptomorphines • Omomyines • Microchoerines • Asian Omomyids
- Tarsiids 313
- Omomyids and Later Primates 313
- Adaptive Radiations of Eocene Prosimians 315
- Phyletic Relationships of Adapids and Omomyids 318
- Bibliography 319

## TWELVE

**Early Anthropoids and Fossil Platyrrhines**

- Possible Early Higher Primates 326
- Fossil Primates from Fayum, Egypt 326
  - Parapithecids • Propithecids • *Oligopithecus*
- The Fayum Primates in Anthropoid Evolution 340
- Fossil Platyrrhines 344
- Summary of Fossil Platyrrhines 349
- Platyrrhine Origins 351



Prosimian Origins of Anthropoids	354
Early Anthropoid Evolution	354
Bibliography	355

## THIRTEEN

**Fossil Apes**

Early and Middle Miocene Apes from Africa	363
Adaptive Radiation of East African Fossil Apes	373
Phyletic Relationships of Early Miocene Apes	373
Eurasian Fossil Apes	376
Pliopithecids • <i>Oreopithecus</i> • Dryopithecines and Pongines	
The Evolution of Living Hominoids	388
Bibliography	391

## FOURTEEN

**Fossil Old World Monkeys**

Victoriapithecids: The Earliest Old World Monkeys	397
Fossil Cercopithecids	401
Fossil Cercopithecines • Fossil Colobines	
Summary of Fossil Cercopithecoids	409
Bibliography	411

## FIFTEEN

**Hominids, the Bipedal Primates**

Genus <i>Australopithecus</i>	416
<i>Australopithecus afarensis</i> • <i>Australopithecus africanus</i> • <i>Australopithecus robustus</i> • <i>Australopithecus boisei</i> • <i>Australopithecus aethiopicus</i>	
Australopithecine Adaptations and Hominid Origins	426
Phyletic Relationships of Early Hominids	433
Genus <i>Homo</i>	435
<i>Homo habilis</i> • <i>Homo erectus</i> • <i>Homo sapiens</i>	
Human Phylogeny	441
Humans as an Adaptive Radiation	443
Bibliography	444

## SIXTEEN

**Patterns in Primate Evolution**

Primate Adaptive Radiations	449
Body Size Changes • Dietary Diversity • Locomotor Diversity	
Patterns in Primate Phylogeny	455
Primate Evolution at the Species Level	456
Primate Extinctions	459
Climatic Changes • Competition • Predation • Limiting Primate Extinctions	
Bibliography	463

Glossary	465
Classification of Order Primates	471
Index	475

# 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