ANTH 374: BIRTH TO DEATH -THE ANTHROPOLOGY OF PRIMATE CULTURE AND BEHAVIOR (FORTUNATO)



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ANTH 374: Birth to Death -The Anthropology of Primate Culture and Behavior (Fortunato)

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CHAPTER OVERVIEW

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SECTION OVERVIEW

1.1: Introduction to Biological Anthropology

Katie Nelson, Ph.D., Inver Hills Community College
Lara Braff, Ph.D., Grossmont College
Beth Shook, Ph.D., California State University, Chico
Kelsie Aguilera, M.A., Leeward Community College

Learning Objectives

- Define anthropology and the main anthropological approaches.
- Describe the origins and early development of anthropology.
- Identify the four subdisciplines of anthropology and specify the focus of each one.
- Define biological anthropology, describe its key questions, and identify major subfields.
- Explain key components of the scientific method.
- Differentiate between hypotheses, theories, and laws.
- Differentiate science from other ways of knowing.

The first time one of the authors [Katie Nelson] heard of biological anthropology, she was a first-year college student at Macalester College in Saint Paul, Minnesota, taking her first-ever anthropology course. Before she enrolled in the class she didn't really know what *anthropology* meant. She knew it had something to do with people, but didn't know how it all fit together. The course description appealed to her, so she signed up. She quickly learned that anthropology was the study of humans and that it was an incredibly broad discipline that included explorations of cultural diversity, human origins, past human societies, and human languages, among a great many other subjects. She had always been interested in learning about people. She enjoyed observing the different ways people interacted in public spaces, like the mall or the zoo. She enjoyed learning Spanish in high school and loved listening to how people who spoke different languages produced different sounds. She was curious about how people inherited unique characteristics from their parents and was especially intrigued by immigration and migration and what caused people to uproot themselves and move to another part of the world. During the second week of class she began to learn about biological anthropology and some of the leading theories for how and why ancient humans left Africa and migrated throughout the world. As she sat in class, she vividly remembers imagining a small group of ancient humans walking barefoot together through the African savannah. She imagined what they wore, what their language sounded like, how they held hands, how they shared food, and so on. She wondered why they were migrating and what they would miss about their homeland. She was hooked on anthropology!

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Katie Nelson

Katie Nelson is an instructor of anthropology at Inver Hills Community College. Her research focuses on migration in human history and citizenship(s), identity, belonging and state mechanisms of migrant control in the contemporary United States, Mexico, and Morocco.

She received her B.A. in anthropology and Latin American studies from Macalester College, her M.A. in anthropology from the University of California, Santa Barbara, an M.A. in education and instructional technology from the University of Saint Thomas, and her Ph.D. from CIESAS Occidente (Centro de Investigaciones y Estudios Superiores en Antropología Social –Center for Research and Higher Education in Social Anthropology), based in Guadalajara, Mexico.

Katie views teaching and learning as central to her practice as an anthropologist and as mutually reinforcing elements of her professional life. She is the former chair of the Teaching Anthropology Interest Group (2016–2018) of the General Anthropology Division of the American Anthropological Association and currently serves as the online content editor for theTeaching and Learning Anthropology Journal. She has contributed to several open access textbook projects, both as an author and an editor, and views the affordability of quality learning materials as an important piece of the equity and inclusion puzzle in higher education.

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Lara Braff is an instructor of anthropology at Grossmont College, where she teaches cultural anthropology and biological anthropology courses. She received her B.A. in anthropology and Spanish from the University of California at Berkeley and both her M.A. and Ph.D. in comparative human development from the University of Chicago, where she specialized in medical anthropology. Her research has focused on social identities and disparities in the context of reproduction and medicine in Mexico and the U.S..

Lara's concerns about the social ramifications of inequality have guided her research projects, teaching practices, and involvement with open access projects like this textbook. Recently, motivated by the desire to make college more affordable and accessible to all students, she has been serving as co-coordinator of Grossmont College's Open Educational Resources (OER) and Zero Textbook Cost (ZTC) degree initiatives.

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Beth enjoys teaching courses in multiple subdisciplines, as well as mentoring graduate students in teaching. Additionally, she coleads Chico State's Affordable Learning Solutions (CAL$) program, is committed to programs that prioritize diversity, and serves on the Society for Anthropology in Community Colleges (SACC) Executive Board as vice president for Membership and Development & Regional Networks chair.

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Kelsie Aguilera is an assistant professor of anthropology at Leeward Community College. Located on the island of O'ahu, Leeward Community College is part of the University of Hawai'i System and holds a special commitment to Native Hawaiian education. At Leeward, Kelsie teaches anthropology courses in all of the subdisciplines and serves on the Open Educational Resources committee. Committed to the open-door mission of community colleges, she previously taught anthropology at Miami-Dade College.

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For Further Exploration

American Anthropological Association website: https://www.americananthro.org/

Partners in Health: https://www.pih.org/

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1.1.1: What is Anthropology?

Why are people so diverse? Some people live in the frigid Arctic tundra, others in the arid deserts of sub-Saharan Africa, and still others in the dense forests of Papua New Guinea. Human beings speak more than 6,000 distinct languages. Some people are barely five feet tall while others stoop to fit through a standard door frame. In some places, people generally have very dark skin, in other places, people are generally pale. In some societies, eating pig is strictly prohibited; in others, pork is a rather ordinary food. What makes people differ from one another? What do we all share in common? How are humans different from other primates? How have primates adapted to different places? How and why did humans develop in the first place? These are some of the questions anthropologists try to answer.



Figure 1.1.1.1: Despite the many evident differences among people, humans are among the most genetically similar species.

Derived from Greek, the word “anthropos” means “human” and “logy” refers to the “study of.” Therefore anthropology, by definition, is the study of humans. Anthropologists are not the only scholars to focus on the human condition; biologists, sociologists, psychologists, and others also examine human nature and societies. However, anthropologists uniquely draw on four key approaches to do their research: **holism**, comparison, dynamism, and fieldwork. Anthropology is an incredibly broad and dynamic discipline. It studies humanity by exploring our past and our present and all of our biological and cultural complexity.

Holism

Anthropologists are interested in the *whole* of humanity, in how various aspects of biological or cultural life intersect. One cannot fully understand what it means to be human by studying a single aspect of our complex bodies or societies. By using a holistic approach, anthropologists ask how different aspects interact with and influence one another. For example, a biological anthropologist studying monkeys in South America might consider the species’ physical adaptations, foraging patterns, ecological conditions, and interactions with humans in order to answer questions about their social behaviors. By understanding how nonhuman primates behave, we discover more about ourselves: after all, as you will learn in this book, humans *are* primates! A cultural anthropologist studying marriage in a small village in India might consider local gender norms, existing family networks, laws regarding marriage, religious rules, and economic requisites in order to understand the particular meanings of marriage in that context. By using a holistic approach, anthropologists appreciate the complexity of any biological, social, or cultural phenomenon.



Figure 1.1.1.2: By using a holistic approach, anthropologists learn how different aspects of humanity interact with and influence one another.

As we will discuss in more detail, anthropology itself is a holistic discipline, comprised (in the United States) of four major areas of study called **subdisciplines**: cultural anthropology, biological anthropology, linguistic anthropology, and archaeology. We need all four subdisciplines in order to understand the human experience, which involves culture, language, and biological and social adaptations, as well as our history, evolution, and relationship to our closest living relatives: nonhuman primates.

Comparison

Anthropology is a comparative discipline: anthropologists compare and contrast data in order to understand what all humans have in common, how we differ, and how we have changed over time. The comparative approach can be historical: How do humans today differ from ancient *Homo sapiens*? How has Egyptian society changed since the building of the great pyramids? How is the English language adapting to new modes of communication like smartphones? The comparative approach is also applied to sociocultural phenomena. We can compare the roles of men and women in different societies or different religious traditions within a given society. Some anthropologists compare different primate species, investigating traits shared by all primates (including humans!) or identifying traits that distinguish one primate group from another. Unlike some other disciplines that also use comparative approaches, anthropologists do not just consider our own species or society. Our comparisons span societies, cultures, time, place, and species.

Dynamism

Humans are one of the most dynamic species. Our ability to change, both biologically and culturally, has enabled us to persist over the course of millions of years, and to thrive in many different environments.

Depending on their research focus, anthropologists ask about all kinds of changes: short-term or long-term, temporary or permanent, cultural or biological. For example, a cultural anthropologist might look at how people in a relatively isolated society change in the context of globalization, the process of interaction and interdependence among different nations and cultures of the world. A linguistic anthropologist might ask how a new form of language, like Spanglish, emerges. An archaeologist might ask how climate change influenced the emergence of agriculture. A biological anthropologist might consider how diseases affecting our ancestors led to changes in their bodies. All these examples highlight the dynamic nature of human bodies and societies. While we differ from our ancestors who lived hundreds of thousands of years ago, we share with them this capacity for change.

Fieldwork

Throughout this book, you will read examples of anthropological research that will take you around the world. Anthropologists do not only work in laboratories, libraries, or offices. To collect data, they go to where their data lives, whether it is a city, village, cave, tropical forest, or desert. At their field sites, anthropologists collect data which, depending on subdiscipline, may be interviews with local peoples, examples of language in use, skeletal remains, or human cultural remains like potsherds or stone tools. While anthropologists ask an array of questions and use diverse methods to answer their research questions, they share this commitment to conducting their research out of their offices and in the field.



Figure 1.1.1.3: Anthropologist Katie Nelson conducting fieldwork among undocumented Mexican immigrant college students.

A Brief History of Anthropology

Imagine only interacting with people who looked, spoke, and acted like you. Now, how would you begin to understand a seemingly new group of people? As people first began to explore the world, they grappled with how to make sense of human differences. Many were adventurers, missionaries, or traders, motivated by a desire to explore, spread their religion, or acquire wealth. All of them were familiar with only one way of life—their own. It was, therefore, through the lens of their own culture that they viewed people they met during their travels.



Figure 1.1.1.4: Statue of Zhang Qian in Chenggu, China. Zhang Qian is still celebrated today in China as an important diplomat and pioneer of the silk road.

One of the first examples of someone who attempted to systematically study and document cultural differences among different peoples is Zhang Qian (Chang Ch'ien 164 BC – 113 BC). Born in the second century BCE in Hanzhong, China, Zhang was a military officer who was assigned by Emperor Wu of Han to travel through Central Asia, going as far as what is today Uzbekistan. He spent more than 25 years traveling and recording his observations of the peoples and cultures of Central Asia (Wood 2004). The Emperor used this information to establish new relationships and cultural connections with China's neighbors to the West. Zhang discovered many of the trade routes used in the Silk Road and introduced many new cultural ideas, including Buddhism, into Chinese culture.



Figure 1.1.1.5: An illustration of Abu Abdullah Muhammad Ibn Battuta in Egypt from Jules Verne's book Discovery of the Earth.

Another early traveler of note was Abu Abdullah Muhammad Ibn Battuta (known most widely as *Ibn Battuta*) (1304-1369). Ibn Battuta was an Amazigh (Berber) Moroccan Muslim scholar. Over a period of nearly 30 years during the fourteenth century, Ibn Battuta's travels covered nearly the whole of the Islamic world, including parts of Europe, sub-Saharan Africa, India, and China. Upon his return to the Kingdom of Morocco, he documented the customs and traditions of the people he encountered in a book called *Tuhfat al-anzar fi gharaaib al-amsar wa ajaaib al-asfar* (A Gift to those who Contemplate the Wonders of Cities and the Marvels of Traveling), but became commonly known as *Al Rihla*, which means "travels" in Arabic (McIntosh-Smith 2003: ix). This book became part of a genre of Arabic literature that included descriptions of the people and places visited along with commentary about the cultures encountered. Some scholars consider *Rihla* to be among the first examples of early pre-anthropological writing.

Later, from the 1400s through 1700s, during the so-called "Age of Discovery," Europeans began to not only explore the world but also colonize it. Europeans exploited natural resources and human labor, exerting social and political control over people they encountered. New trade routes, along with the slave trade, fueled a growing European empire, while forever disrupting previously independent cultures in the Old World. European **ethnocentrism**—the belief that one's own culture is better than others—was used to justify the subjugation of non-European societies.

As European empires expanded, new ways of understanding the world and its people arose. Beginning in the eighteenth century in Europe, the Age of Enlightenment was a social and philosophical movement that privileged science, rationality, and empiricism while critiquing religious authority. This crucial period of intellectual development planted the seeds for many academic disciplines, including anthropology. It gave ordinary people the capacity to learn through observation and experience: *Anyone* could ask questions and use rational thought to discover things about the natural and social world.

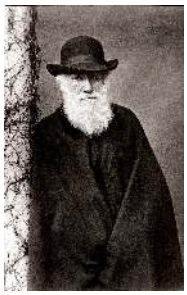


Figure 1.1.1.6: Charles Darwin, circa 1881.

For example, Charles Lyell (1797–1875), a geologist, would observe layers of rock and argue that Earth's surface must have changed gradually over long periods of time, such that it could not be only 6,000 years old (as the Young Earth interpretation in the Bible contends). Charles Darwin (1809–1882), a naturalist and biologist, would observe similarities between fossils and living specimens, leading him to argue that all life is descended from a common ancestor. Philosopher John Locke (1632–1704) would contemplate the origins of society itself. He wrote that people lived in relative isolation until they agreed to form a society in which the government would protect their personal property.

These radical ideas about the earth, evolution, and society influenced early social scientists into the nineteenth century. For example, Herbert Spencer (1820–1903), inspired by scientific principles, used biological evolution as a model to understand social evolution: just as biological life evolved from simple to complex multicellular organisms, he postulated that societies "evolve" to become larger and more complex. Lewis Henry Morgan (1818–1881) argued that all societies "progress" through the same stages of development: savagery—barbarism—civilization. Societies were classified into these stages based on their kinship patterns, technologies, subsistence patterns, and so forth. So-called savage societies, ones that used rudimentary tools and foraged for food, were said to be stalled in their mental and moral development.

Ethnocentric ideas, like those of Morgan, were challenged by anthropologists in the early twentieth century in both Europe and the United States. During World War I, Bronislaw Malinowski (1884–1942), a Polish anthropologist, became stranded on the Trobriand Islands, where he started to do **participant-observation** fieldwork: the method of immersive, long-term fieldwork that cultural anthropologists use today. By living with and observing the Trobrianders, he realized that their culture was not "savage," but rather fulfilled the needs of the people. He developed a theory to explain human cultural diversity: Each culture functions to satisfy the specific biological and psychological needs of its people. While this theory has been critiqued for overemphasizing individuals apart from culture, it was an early attempt to view other cultures in more relativistic ways.



Figure 1.1.1.7: Franz Boas, circa 1915

Around the same time in the United States, Franz Boas (1858–1942), widely regarded as the founder of American anthropology, developed the cultural relativistic approach: the view that cultures differ but are not better or worse than one another. In his critique of ethnocentric views, Boas insisted that physical and behavioral differences among so-called racial groups in the United States were shaped by environmental and social conditions, not biology. In fact, he argued, culture and biology are distinct realms of experience: Human behaviors are socially learned, contextual, and flexible, not innate. Further, Boas worked to transform anthropology into a professional and **empirical** academic discipline that integrated the four subdisciplines: cultural anthropology, linguistic anthropology, archaeology, and biological anthropology.

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1.1.2: The Subdisciplines

Because human experiences are varied and complex, we need a diversified tool kit to study them. Anthropology therefore comprises four subdisciplines: Some are more scientific (like biological anthropology), while others are more humanistic (like cultural anthropology). The scientific subdisciplines tend to use the scientific method to develop theories that explain human origins, evolution, material remains, or behaviors. The humanistic subdisciplines tend to use observational methods and interpretive approaches to understand human beliefs, languages, behaviors, cultures, and social organization. Findings from all four subdisciplines contribute to a multifaceted appreciation of human bio-cultural experiences, past and present.

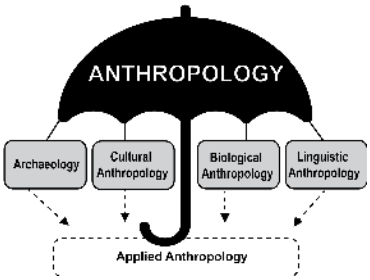


Figure 1.1.2.1: The discipline of anthropology has four subdisciplines as well as an applied dimension.

Cultural Anthropology

Cultural anthropologists focus on similarities and differences among living societies. They suspend their own sense of what is "normal" in order to understand the perspectives of the people they study (**cultural relativism**). They learn these perspectives through participant-observation fieldwork: a method that involves living with, observing, and learning from the people one studies. Beyond describing another way of life, cultural anthropologists ask broader questions about humankind: Are human emotions universal or culturally specific? Does globalization make us all the same or do we maintain cultural differences? For cultural anthropologists, no aspect of human life is outside their purview: They study art, religion, healing, natural disasters, video gaming, even pet cemeteries. While many cultural anthropologists are intrigued by human diversity, they realize that people around the world share much in common.



Figure 1.1.2.2: Margaret Mead, circa 1948.

One famous American cultural anthropologist, Margaret Mead (1901–1978), conducted several cross-cultural studies of gender and socialization practices. In the early twentieth century in the United States, people wondered if the emotional turbulence of American adolescence was caused by the biology of puberty (and thus natural and universal) or something else. To find out, Mead set off for the Samoan Islands, where she lived for several months getting to know Samoan teenagers. She learned that Samoan adolescence was not angst-ridden (like it was in the United States), but rather a relatively tranquil and happy life stage. Upon returning to the United States, Mead wrote *Coming of Age in Samoa*, a best-selling book that was both sensational and scandalous (Mead 1928). In it, she critiqued U.S. parenting as overly restrictive, and contrasted it to Samoan parenting, which allowed teenagers to freely explore their community and even their sexuality. Ultimately, she argued that nurture (i.e., socialization) more than nature played a key role in the experience of child development.

Cultural anthropologists do not always travel far to provide insight into human experience. In the 1980s, American anthropologist Philippe Bourgois (1956–) wanted to understand how pockets of extreme poverty persist amid the wealth and overall high quality of life in the United States. To answer this question, he lived with Puerto Rican crack dealers in East Harlem, contextualizing their experiences both historically (in terms of socioeconomic dynamics in Puerto Rico and in the United States) and presently (in terms of social marginalization and institutional racism). Rather than blame crack dealers for their poor choices or blame our society for perpetuating inequality, he argued that both individual choices and social inequality can trap people in the overlapping worlds of drugs and poverty (Bourgois 2003).

Linguistic Anthropology

Language is a defining trait of human beings. While other animals have communication systems, only humans have complex, symbolic languages—more than 6,000 of them! Human language makes it possible to teach and learn, to plan and think abstractly, to coordinate our efforts, and to contemplate even our own demise. Linguistic anthropologists ask questions like: How did language first emerge? How has it evolved and diversified over time? How has language helped us succeed as a species? How does language indicate social identity? How does language influence our views of the world? If you speak two or more languages, you may experience how language affects you. For example, in English, we say: "I love you." But Spanish speakers use different terms—"te amo," "te adoro," "te quiero," and so on—to convey different kinds of love: romantic love, platonic love, maternal love, etc. The Spanish language arguably expresses more nuanced versions of love than the English language



Figure 1.1.2.3: From the moment they are born, children learn through language and nonverbal forms of communication.

One intriguing line of linguistic anthropological research focuses on the relationships between language, thought, and culture. It may seem intuitive that our thoughts come first; after all, we like to say, "Think before you speak." However, according to the **Sapir-Whorf hypothesis** (also known as linguistic relativity), the language you speak allows you to think about some things and not other things. When Benjamin Whorf (1897–1941) studied the Hopi language, he not only found word-level differences, but also grammatical differences between Hopi and English tenses. He wrote that Hopi has no grammatical tenses to convey the passage of time. Rather, Hopi language only indicates whether or not something has "manifested." Whorf argued that English grammatical tenses (past, present, future) inspire a linear sense of time, while Hopi language inspires a cyclical experience of time (Whorf 1956). Some critics, like German American linguist Ekkehart Malotki (1938–), refute Whorf's theory, arguing that Hopi do have linguistic terms for time and that a linear sense of time is natural and perhaps universal. At the same time, Malotki recognized that English and Hopi tenses differ, albeit in ways less pronounced than Whorf proposed (Malotki 1983).

Other linguistic anthropologists track the emergence and diversification of languages, while others focus on language use in today's social contexts. Still others explore how language is crucial to socialization: children learn their culture and social identities through language and nonverbal forms of communication (Ochs and Schieffelin 2012).

Archaeology

Archaeologists focus on the material past: the tools, food, pottery, art, shelters, seeds, and other objects left behind by people. **Prehistoric archaeologists** recover and analyze these materials to reconstruct the lifeways of past societies that lacked writing. They ask specific questions like: How did people in a particular area live? What did they eat? What happened to them? They ask general questions about humankind: When and why did humans first develop agriculture? How did cities first develop? What type of interactions did prehistoric people have with their neighbors?

One key method that archaeologists use to answer their questions is excavation—a method of careful digging and removing of dirt and stones to uncover material remains while recording their context. Archaeological research spans millions of years from human origins to the present. For example, Kathleen Kenyon (1906–1978), a British archaeologist, was one of few women working in this field in the 1940s. While excavating at Jericho (which dates back to 10,000 BCE), she discovered city structures and cemeteries built during the Early Bronze Age (3,200 yBP in Europe). Based on her findings, she argued that Jericho is the oldest city continuously occupied by different groups of people (Kenyon 1979).



Figure 1.1.2.4: Archaeologists, including Kathleen Kenyon, have helped unearth the foundations of ancient dwellings at Jericho.

Historical archaeologists study recent societies using material remains to complement the written record. For example, the Garbage Project, which began in the 1970s, is an archaeological project based in Tucson, Arizona. It involves excavating a contemporary landfill as if it were a conventional dig site. Archaeologists found a difference between what people say they throw out and what is actually in their trash. In fact, many landfills hold large amounts of paper products and construction debris (Rathje and Murphy 1992). This finding has practical implications for creating more environmentally sustainable waste-disposal practices.

Biological Anthropology

Biological anthropology, which will be thoroughly introduced later in this chapter, is the study of human origins, evolution, and variation. Some biological anthropologists focus on our closest living relatives: monkeys and apes. They examine the biological and behavioral similarities and differences between nonhuman primates and human primates (us!). Other biological anthropologists focus on extinct human species, asking questions like: What did our ancestors look like? What did they eat? When did they start to speak? And, how did they adapt to new environments?



Figure 1.1.2.5: Chimpanzees are the nonhuman primate that is most closely related to humans.

Many biological anthropologists explore how human genetic and phenotypic (observable) traits vary in response to environmental conditions. For instance, Nina Jablonski (1953–) asks why darker skin pigmentation is more prevalent in high ultraviolet (UV) contexts (like Central Africa), while lighter skin pigmentation is more prevalent in low UV contexts (like Nordic countries). She explains this pattern in terms of the interplay among skin pigmentation, UV radiation, folic acid, and vitamin D. In brief, UV radiation breaks down folic acid, which is essential to DNA and cell production. Dark skin helps to block UV, thereby protecting the body's folic acid reserves in high-UV contexts. Light skin evolved when humans migrated out of Africa to low-UV contexts, where dark skin blocks too much UV radiation, compromising the body's ability to absorb vitamin D from the sun (vitamin D is essential to calcium absorption and a healthy skeleton). Jablonski shows that the spectrum of skin pigmentation that we see today evolved to balance UV exposure with the bodily need for vitamin D and folic acid (Jablonski 2012).



Figure 1.1.2.6: Human skin color ranges from dark brown to light pink.

While some biological anthropologists study **hominins** (modern-day humans and human ancestors), others focus on nonhuman primates. For example, Jane Goodall (1934–) has devoted her life to studying wild chimpanzees (Goodall 1996). Beginning in the 1960s when she began her research in Tanzania, Goodall challenged widely held assumptions about the inherent differences between humans and apes. At the time, it was assumed that monkeys and apes lacked the social and emotional traits that made human beings such exceptional creatures. However, Goodall discovered that, like humans, chimpanzees also make tools, socialize their young, have intense emotional lives, and form strong maternal-infant bonds. Her work highlights the value of field-based research in natural settings as it can reveal the complex lives of nonhuman primates. Throughout this book, we will learn about many examples of biological anthropological research that explores our earliest ancestors, our evolution, and our nonhuman primate cousins.

Applied Anthropology

Sometimes considered a fifth subdiscipline, applied anthropology involves the practical application of anthropological theories, methods, and findings to solve real-world problems. Applied anthropologists are employed outside of academic settings, in both the public and private sectors, including business or consulting firms, advertising companies, city government, law enforcement, the medical field, nongovernmental organizations, and even the military.

Applied anthropologists span the subdisciplines. An applied archaeologist might work in cultural resource management to assess a potentially significant archaeological site unearthed during a construction project. An applied cultural anthropologist could work for a technology company that seeks to understand the human-technology interface in order to design better tools.

Medical anthropology is an example of both an applied and theoretical area of study that draws on all four subdisciplines to understand the interrelationship of health, illness, and culture. Rather than assume that disease resides only within the individual body, medical anthropologists explore the environmental, social, and cultural conditions that impact the *experience* of illness. For example, in some cultures, people believe that illness is caused by an imbalance within the community. Therefore, a communal response, such as a group healing ceremony, is necessary to restore the health of the person *and* the group. In other cultures, like mainstream U.S. society, people typically go to a doctor to find the biological cause of an illness and then take medicine to restore the individual body.



Figure 1.1.2.7: Paul Farmer in Haiti (right).

Trained as both a physician and medical anthropologist, Paul Farmer (1959–) demonstrates the potential of applied anthropology. During his college years in North Carolina, Farmer's interest in the Haitian migrants working on nearby farms inspired him to visit Haiti. There, he was struck by the poor living conditions and lack of health care facilities. Eventually, as a physician, he would return to Haiti to treat diseases, like tuberculosis and cholera, that were rarely seen in the United States. As an anthropologist, he would contextualize the suffering of his Haitian patients in relation to the historical, social, and political forces that impact Haiti, the poorest country in the Western Hemisphere (Farmer 2006). Today, he not only writes academic books about human suffering, he also takes action. Through the work of Partners in Health, a nonprofit organization that he cofounded, he has opened health clinics in many resource-poor countries and trained local staff to administer care. In this way, he applies his medical and anthropological training to improve people's lives.

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1.1.3: What is Biological Anthropology

The focus of this book is the anthropological subdiscipline of biological anthropology, which is the study of the human species from a biological perspective. Biological anthropology uses a scientific and evolutionary approach to answer many of the same questions all anthropologists are concerned with: What does it mean to be human? Where do we come from? Who are we today? Biological anthropologists are concerned with exploring how humans vary biologically, how humans adapt to their changing environments, and how humans have evolved over time and continue to evolve today. Some biological anthropologists also study nonhuman primates to learn about what we have in common and how we differ.

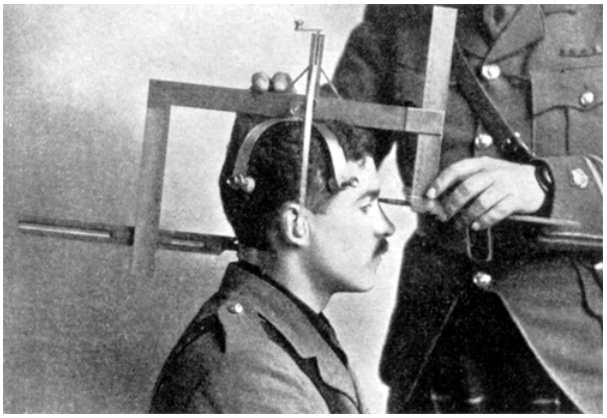


Figure 1.1.3.1: An anthropometric device used to measure a subject's head, circa 1913.

You may have heard biological anthropology referred to by another name—physical anthropology. Physical anthropology is an area of research that dates to as far back as the eighteenth century, when it focused mostly on physical variation among humans. Some early physical anthropologists were also physicians interested in comparing and contrasting human skeletons. These researchers dedicated themselves to measuring bodies and skulls (anthropometry and craniometry) in great detail. Many also acted under the misguided and oftentimes racist belief that human biological races existed and it was possible to differentiate between, or even rank, such races by measuring differences in human anatomy. Most anthropologists today agree that there are no biological human races and that all humans alive today are members of the same species and subspecies, *Homo sapiens sapiens*. We recognize that the differences we can see between peoples' bodies are due to a wide variety of factors, including our environment, our diet, the activities we engage in, and our genetic makeup.

The subdiscipline has changed a great deal since these early years. Biological anthropologists no longer set out to identify human differences in order to assign people to groups, like races. The focus is instead understanding how and why human and primate variation developed through evolutionary processes. The name for the subdiscipline has transitioned in recent years to reflect these changes. Many believe the term biological anthropology better reflects the subdiscipline's focus today, which includes genetic and molecular research. Nevertheless, the term physical anthropology is still common.

The Scope of Biological Anthropology

Just as anthropology as a discipline is wide ranging and holistic, so too is the subdiscipline of biological anthropology. There are at least six **subfields** within biological anthropology. Each subfield focuses on a different dimension of what it means to be human from a biological perspective. Through their varied research in these subfields, biological anthropologists try to answer the following key questions:

- What is our place in nature? How are we related to other organisms? What makes us unique?
- What are our origins? What influenced our evolution?
- How and when did we move/migrate across the globe?
- How are humans around the world today different from and similar to each other? What influences these patterns of variation? What are the patterns of our recent evolution and how do we continue to evolve?

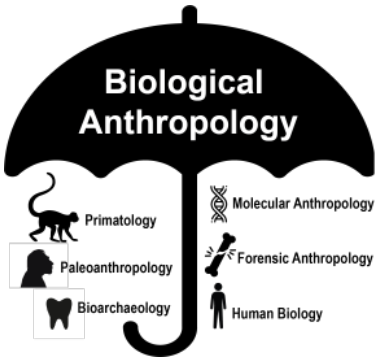


Figure 1.1.3.2: Biological anthropology has at least six subfields.

The terms *subfield* and *subdiscipline* are very similar and can be confusing because they are often used interchangeably. In this book we use *subdiscipline* to refer to the four major areas of focus that make up the discipline of anthropology: biological anthropology, cultural anthropology, archaeological anthropology, and linguistic anthropology. When we use the term *subfield* we are referring to the different specializations within biological anthropology. These subfields include primatology, paleoanthropology, molecular anthropology, bioarchaeology, forensic anthropology, and human biology.

Primatology

Primatologists study the anatomy, behavior, ecology and genetics of living and extinct nonhuman primates, including apes, monkeys, tarsiers, lemurs, and lorises, because nonhuman primates are our closest living biological relatives. The research done by primatologists gives us insights into how evolution has shaped our species and primates in general. Through such studies we have learned that all primates share a suite of traits. Primates, for instance, have nails instead of claws, have hands that can grasp and manipulate objects, invest great amounts of time and energy in raising just a few offspring, and have complex social behaviors.



Figure 1.1.3.3: Adult male mountain gorillas feeding on insects. Notice how similar his fingers are to your own fingers.

Similar to Jane Goodall's studies of wild chimpanzees, Dian Fossey's research among mountain gorillas provided scientists with some illuminating insights into our primate cousins. She learned, for instance, that gorillas are like humans in that they have families and form strong maternal-infant relationships. Gorillas mourn the death of their group members, and also exhibit behaviors similar to humans such as playing and tickling. Importantly, the work of Dian Fossey, Jane Goodall, Karen B. Strier (see Appendix B), and others focus on primate conservation: They have brought attention to the fact that 60% of primates are currently threatened with extinction (Estrada et al. 2017).

Paleoanthropology

Paleoanthropologists study human ancestors from the distant past to learn how, why, and where they evolved. Because these ancestors lived before there were written records, paleoanthropologists have to rely on various types of physical evidence to come to their conclusions. This evidence includes fossilized remains (particularly fossilized bones), artifacts such as stone tools, and the

contexts in which these items are found. Paleoanthropologists have made some monumental discoveries that have shaped the way we understand **hominin** evolution (hominin refers to humans and fossil relatives that are more similar to us than chimpanzees).



Figure 1.1.3.4: Donald Johanson and an *Australopithicus* fossil skull.

One such discovery was made in Ethiopia in 1974 by paleoanthropologist Donald C. Johanson. He found the remains of a 3.2-million-year-old fossilized skeleton he named Lucy (she was named after the Beatles song "Lucy in the Sky with Diamonds," which the archaeologists played repeatedly at the celebration the evening after her discovery). Lucy was a remarkable find because she represented a new hominin species, *Australopithecus afarensis*, and the skeleton was over 40% complete. Like humans, she was **bipedal** (walked on two legs) and likely used tools. However she had a much smaller brain than humans, larger teeth and likely spent time in trees and on the ground. She was, in many ways, a transitional species between humans and earlier primates.

Since the discovery of Lucy, several hundred more *Australopithicus* fossils have been found in Africa, as you will learn more about in chapter nine. From these finds, we know that many *Australopithicus* species flourished for millions of years. Some of these species likely led to our genus (*Homo*), while others appear to have died off. These findings helped us learn that human evolution did not occur in a simple, straight line, but branched out in many directions. Most branches were evolutionary "dead ends." Humans are now the only hominins left living on planet Earth. Paleoanthropologists frequently work together with other scientists such as archaeologists, geologists, and paleontologists to interpret and understand the evidence they find. Paleoanthropology is a dynamic subfield of biological anthropology that contributes significantly to our understanding of human origins and evolution.

Molecular Anthropology

Molecular anthropologists use molecular techniques (primarily genetics) to compare ancient and modern populations and to study living populations of humans and nonhuman primates. By examining DNA sequences in different populations, molecular anthropologists can estimate how closely related two populations are, as well as identify population events, like a population decline, that explain the observed genetic patterns. This information helps scientists trace patterns of migration or identify how people have adapted to different environments over time.

Some exciting work that molecular anthropologists are doing today is studying the genetic material they find in ancient specimens. From this work we have learned, for instance, that many people in the world today have inherited some DNA from Neanderthals and/or a newly discovered species known as Denisovans. This tells us that at some point in our ancient past our modern human ancestors mated with Neanderthals and Denisovans and their genes were passed down to us. Moreover, it is now believed some of these genes helped our human ancestors survive.

From the work of molecular anthropologists we have also learned which genes distinguish us genetically from our closest living relatives: chimpanzees, bonobos, and gorillas. In the case of chimpanzees, our genomes are somewhere between 96% and 99% identical (Prufer et al. 2012; Relethford and Bolnick 2018). Yet that 2-4% contributes to a lot of physical (morphological) and behavioral differences! Molecular anthropology is a field changing quickly as new techniques and discoveries shape our understanding of ourselves and our nonhuman primate cousins.

Bioarchaeology

Bioarchaeologists study human skeletal remains and the soils and other materials found in and around the remains. They use the research methods of skeletal biology, mortuary studies, osteology, and archaeology to answer questions about the lives and lifeways of past populations. Through studying the bones and burials of past peoples, bioarchaeologists search for answers to how people lived and died. For example, bioarchaeologists can estimate the sex, height, and age at which someone died. They can also gather clues about their lifestyle based on the skeleton, since bones respond to muscle use and developed muscle attachments may indicate extensive muscle use. Most bioarchaeologists study not just individuals, but populations, to reveal biological and cultural patterns.



Figure 1.1.3.5: A model of what Ötzi may have looked like in life.

Bioarchaeologists are also interested in learning about ancient people's health and nutrition, the diseases they suffered from and injuries they suffered. They may also look for clues to what people ate by examining the wear and condition of teeth or, in the case of well-preserved specimens, the residue from their last meals. Chemical studies of bones and teeth can also provide information about people's diets as well as where people lived and moved during their lives. Bioarchaeologists can reconstruct human migration and track the growth or decline of populations by looking for patterns of malnutrition, disease, and activities.

Not all places are ideal for finding well-preserved human remains. Environments that are very cold, very dry, or devoid of oxygen can preserve corpses for many years, sometimes centuries. In 1991, a group of hikers found the body of a man frozen in the Italian Alps. Because of how well-preserved the body was, the discoverers initially thought he might be a hiker who had died several years prior. However, once bioarchaeologists had a chance to study the body, they discovered the man had died around 5,300 years ago! Nicknamed Őtzi, or the Iceman, bioarchaeologists determined he was wearing leggings, a coat, and shoes made of leather and fur when he died. They also discovered he had an arrow embedded in his left shoulder, suffered from osteoporosis, had multiple tattoo patterns throughout his body and was infected by the bacterium *H. pylori*, a common human stomach pathogen that likely gave him significant stomach pain. Researchers later found similarities between the strain of *H. plyori* bacterium that plagued Őtzi and the strains seen today in parts of Central and Southern Asia. Modern-day Europeans have strains of the bacterium that reflect mixtures of both African and Asian strains. This research helped scientists demonstrate that for thousands of years after Őtzi died human groups were migrating all over the world, even returning to Africa and then moving back north again. Research within the subfield of bioarchaeology is continually providing important insights into humanity's past.

Forensic Anthropology

Forensic anthropologists use many of the same techniques as bioarchaeologists to develop a biological profile for unidentified individuals including estimating sex, age at death, height, ancestry, diseases they had, or other unique identifying features. They may also go to a crime or accident scene to assist in the search and recovery of human remains, and/or identify trauma, like fractures, on bones. The popular television program *Bones* told the fictional story of a forensic anthropologist, Dr. Temperance Brennan, who brilliantly interpreted clues from victims' bones and helped solve crimes. While the show includes forensic anthropology techniques and responsibilities, it also includes many inaccuracies. For example, forensic anthropologists generally do not collect trace evidence like hair or fibers, run DNA tests, carry weapons, or solve criminal cases. These researchers play an important role in aiding law enforcement to identify human remains.



Figure 1.1.3.6: A remembrance of the victims of El Mozote Massacre in El Salvador.

Some forensic anthropologists have been called on to interpret the remains of victims of mass murders, such as the case of the town of El Mozote in El Salvador. In December of 1981, during the country's intense civil war, over 1,000 people were brutally killed by the Salvadoran right-wing military in and around a church in the town of El Mozote. Researchers later discovered that the U.S. government, under President Reagan, funded and trained the Special Forces of the Salvadoran Army who perpetrated the massacre. Starting in the mid-1990s, human rights organizations began to investigate the incident as a war crime, and finally, in 2015, a team of forensic anthropologists were called upon to study the bones of the deceased and try to reconstruct what happened at El Mozote

and how the victims died (Binford 2016). Their work provided important clues that helped bring some closure to the families and survivors of this horrible incident. It also provided answers to investigators looking to bring accountability to those responsible.

Forensic anthropology is considered an “applied” area of biological anthropology, since it is a practical application of anthropological theories, methods, and findings to solve real-world problems. While many forensic anthropologists are also academics and work for colleges and universities, some are employed by other agencies. Forensic anthropology is an active area of applied biological anthropology and a career that is useful all over the world.

Human Biology

Many biological anthropologists do work that falls under the label human biology. This type of research is varied, but tends to explore how the human body is impacted by different physical environments, cultural influences, and nutrition. These include studies of **human variation** or the physiological differences among humans around the world. For instance, some humans have the ability to digest lactase in milk into adulthood, and others lack this ability. Some humans have an enhanced ability to resist malarial infections. Some humans tend to be very tall and lean while others are short and stocky. Still others tend to have dark skin and others lighter brown and even pale skin colors.

Some of these anthropologists study **human adaptations** to extreme environments, which includes individual physiological responses and genetic advantages populations develop to help them live there. For example, people born at very high elevations adapt to life in an environment with decreased oxygen. Research has shown that populations that have lived for many generations at very high elevations, such as those in parts of Tibet, Peru, and Ethiopia, have developed long-term physiological adaptations. These include large lungs and chests and enhanced oxygen respiration and blood circulation systems that help them survive in an environment that otherwise might cause life-threatening hypoxia (oxygen deprivation) (Bigham 2016). Some anthropologists believe Tibetans’ adaptation to living in high altitudes, estimated to have occurred in less than 3,000 years, is one of the fastest cases of human evolution in the scientific record!

In addition to studying how humans adapt to their physical environments and vary biologically, some biological anthropologists are interested in how nutrition and disease affect human growth and development. The modern Western diet that is high in processed starches, refined carbohydrates, saturated fats, sugar, and salt is increasingly causing a number of metabolic conditions. As cultural groups around the world begin to replace their traditional diets with these processed food products, they begin to experience a rise in diseases that plague Western societies, such as diabetes, heart disease, and hormonal imbalances. Other biological anthropologists have asked why girls in Western societies have begun to menstruate earlier (sometimes as young as seven years of age). A definitive explanation is still unresolved. Some speculate this may have to do with changes in our diet, while others believe it may also have to do with exposure to chemicals in the environment or other factors. Biological anthropologists engage in a wide range of research that span the breadth of human biological diversity.

The six subfields of biological anthropology—primatology, paleoanthropology, bioarchaeology, molecular anthropology, forensic anthropology, and human biology—all help us understand what it means to be biologically human. From molecular analyses of our cells, to studies of our changing skeleton, to research on our nonhuman primate cousins, biological anthropology helps answer the central question of the larger discipline of anthropology: What does it mean to be human? Despite their different foci, all biological anthropologists share a commitment to using a scientific approach to study how we became the complex, adaptable species we are today.

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1.1.4: Anthropologists as Scientists

Biological anthropologists use the scientific method as a way of learning about the world around them. Many people think of science as taking place in a sterile laboratory, and sometimes it does, but in biological anthropology it also occurs many other places, such as at a research station in Ethiopia, a field site in Tanzania, and a town in El Salvador. To understand how information in this field is established, it is important to recognize what science is (and is not) as well as understand how the scientific method actually works.

Recognizing Science

Science combines our natural curiosity with our ability to experiment so we can understand the world around us and address needs in our communities. Thanks to science, meteorologists can predict the weather, it takes only a relatively small number of farmers to grow enough food to feed our large population, our medicine continues to improve, and over 90% of Americans have a cell phone.

Anyone can participate in science—not just academics. In fact, children are often some of the best scientists. An early, well-known psychologist, Jean Piaget (1896–1980), argued that a child is a "little scientist," internally motivated to experiment and explore their world. This can be seen when an infant repeatedly drops a toy to see if the parent will pick it up, or when a four-year-old sincerely asks "why" again and again. Maria Montessori (1870–1952), an Italian doctor and educator, was interested in how children learn. Through her research, she also recognized that children have natural scientific tendencies. Children have a desire to explore their environment, ask questions, use their imaginations, and learn by doing. In 1907, Montessori opened a school to foster children's natural desire to learn this way. This developed a child-centered teaching method that has spread around the world and is being used in over 22,000 schools today. In anthropology and other scientific fields, the process of learning is more formalized, but scientists still benefit from the curiosity that motivates children and still experience the thrill of discovery.



Figure 1.1.4.1: *Children are true scientists as they explore and test the world around them through sight and touch.*

Science represents both a body of knowledge and the process for learning that knowledge (the scientific method). Scientific claims can, at times, be difficult to distinguish from other information. Science also incorporates a broad range of methods to collect data, adding to the difficulty of knowing what science really is. This section of the chapter will address four key characteristics that help define and recognize science: (1) science studies the physical and natural world and how it works, (2) scientific explanations must be testable and refutable, (3) science relies on empirical evidence, and (4) science involves the scientific community.

Science Studies the Physical and Natural World and How It Works

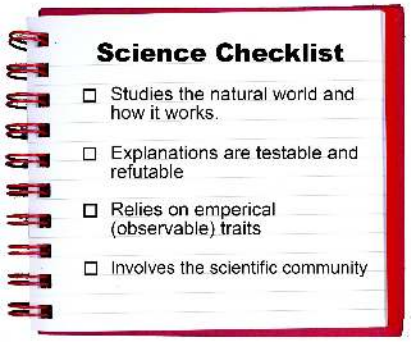


Figure 1.1.4.2: Science checklist.

Our physical and natural universe ranges from very small (e.g., electrons) to the very large (e.g., Earth itself and galaxies beyond it). Scientists often design their research to address how and why natural forces influence our physical and natural word. In biological anthropology, we focus our questions on humans as well as primate species, both living and extinct. We ask questions like: What influences a primate's diet? Why do humans walk bipedally? And did Neanderthals and modern humans interbreed?

There are very few questions that are considered off-limits in science. That being said, the scope of scientific investigation is generally focused on natural phenomena and natural processes and excludes the supernatural. People often regard the supernatural, whether it be a ghost, luck, or god, as working outside the laws of the universe, which makes it difficult to study with a scientific approach. Science neither supports nor contradicts the existence of supernatural powers—it simply does not include the supernatural in its explanations.

Scientific Explanations Must Be Testable and Refutable

The goal of scientists is to identify a research question and then identify the best answer(s) to that question. For example, an excavation of a prehistoric cemetery may reveal that many of the people buried there had unhealed fractures when they died, and the lead anthropologist may ask, "Why did this population experience more broken bones than their neighbors?" There might be multiple explanations to address this question, such as a lack of calcium in their diets, participation in dangerous work, or violent conflict with neighbors; these explanations are considered hypotheses. In the past, you might have learned that a hypothesis is an "educated guess," but in science, hypotheses are much more than that. A scientific hypothesis reflects a scientist's knowledge-based experiences and background research. A **hypothesis** is better defined as an explanation of observed facts; hypotheses explain how and why observed phenomena are the way they are.

Scientific hypotheses should generate expectations that are testable. For example, if the best explanation regarding our prehistoric population was that they were experiencing violent conflict with their neighbors, we should expect to find clues, like weapons or protective walls around their homes, in the anthropological record to support this. Alternatively, if this population did not experience violent conflict with their neighbors, we may eventually be able to gather enough evidence to rule out (refute) this explanation. An important part of science is rigorous testing. Science does not prove any hypothesis. However, a strong hypothesis is one that has strong supporting evidence and has not yet been disproven.

Science Relies on Empirical Evidence

The word "empirical" refers to experience that is verified by observation (rather than evidence that derives primarily from logic or theory). In anthropology, much evidence about our world is collected by observation through fieldwork or in a laboratory. The most reliable studies are based on accurately and precisely recorded observations. Scientists value studies that explain exactly what methods were used, so their data collection and analysis processes are reproducible. This allows for other scientists to expand the study or provide new insights into the observations.

Science Involves the Scientific Community

Contrary to many Hollywood science fiction films, good science is not carried out in isolation in a secret basement laboratory but rather is done as part of a community. Scientists pay attention to what others have done before them, present new ideas to each other, and publish in scientific journals. Most scientific research is collaborative, bringing together researchers with different types of specialized knowledge to work on a shared project. Today, thanks to technology, scientific projects can bring together researchers from different backgrounds, experiences, locations, and perspectives. Most big anthropological questions—"Where did modern humans develop?" "What genetic changes make us uniquely human?" "How did cooperative behavior evolve?"—cannot be addressed with one simple study, but are tested with different lines of evidence and by different scientists over time.

Working within a scientific community supports one of the most valuable aspects of science: that science is self-correcting. Science that is openly communicated with others allows for a system with checks and balances: competing explanations can be proposed and questionable studies can be reevaluated. Ultimately, the belief is that through science the best explanations will stand the test of time.

How Science Works: The Scientific Method

Most students have learned the scientific method as a simple linear, or perhaps circular, process. Textbooks may phrase each step differently, but students usually recognize that the process begins with making observations about the natural world. Another important step is the selection or development of a scientific hypothesis. From the hypothesis a set of predictions can be made, which are then tested by experimentation or by making additional observations. Scientific predictions are often phrased as "if…

then…” statements, such as “If hypothesis A is true, then this experiment will show outcome B.” The results of a scientific study should then either support or reject the hypothesis.

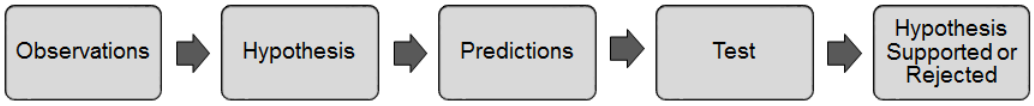


Figure 1.1.4.3: *Simple depiction of the scientific method.*

This relatively simple version of the scientific method is valuable as it highlights the key aspects that should be present in any scientific research experiment or scientific paper. However, this simplistic view of the scientific method does not accurately represent the dynamic and creative side of science, nor does it highlight the complex steps that are incorporated into a scientist’s routine.

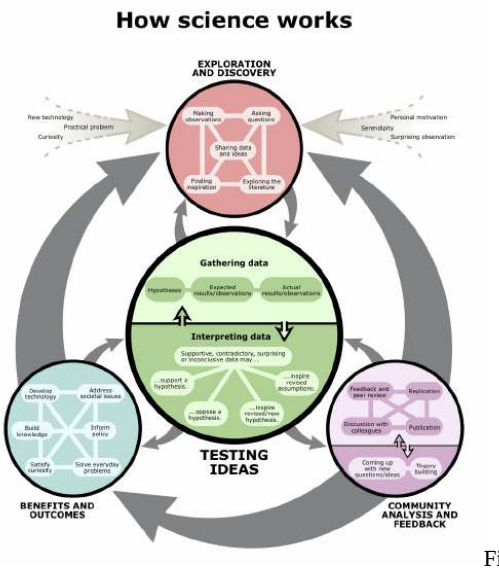


Figure 1.1.4.4: *Complex flow of the scientific method.*

Figure 1.24 provides an alternative representation of the scientific method that emphasizes the many paths to scientific discovery. While still incorporating the key components of making observations, testing ideas, and interpreting results, this chart shows that scientific ideas have many possible starting points and influences, and scientists often repeat steps and circle back around. Gathering evidence does not always rest on experiments in the laboratory. Evaluating data is not always clear-cut, and results are sometimes surprising or inconclusive. Many important discoveries were in fact made by mistake. For example, engineer Percy Spencer accidentally melted a chocolate bar in his pocket with a magnetron, which became the first microwave, and Spencer Silver invented the adhesive for 3M Post-it ® notes while trying to develop a strong glue. The real scientific process is more similar to the philosophy of the animated television character Ms. Frizzle from *The Magic School Bus*, “Take chances, make mistakes, get messy.”

Two key components lacking in the simple version of the scientific method are exploration and discovery. There are many reasons that a scientist might choose a particular research question: they may be motivated by personal experience, struck by something they read about, or inspired by a student’s question in class. Often scientific research reveals more questions than answers, so experienced researchers rarely lack problems to solve. But identifying a research question is just part of the process; most scientists spend more time exploring the literature, sharing ideas, asking questions, and planning their research project than conducting the test itself.

Science itself is a social enterprise that is influenced by cultural issues and values, as well as funding priorities. For example, corporations are the biggest funders of scientific research, followed next by government agencies like the National Science Foundation (which often fund research done by academics at colleges and universities). Those organizations have great influence on what is considered valuable research at any given time. For example, there are many diseases that the World Health Organization (WHO) has classified as “neglected tropical diseases,” including dengue, leprosy, rabies, and hookworm, that affect

an estimated 1 billion people, mostly in impoverished areas. These debilitating diseases can be as deadly as diseases that receive more attention, like AIDS and tuberculosis, but these tropical diseases receive comparatively little funding when it comes to research, drug development, and health care development (Farmer et al. 2013).

Also very important to the scientific process are interactions within the scientific community. Scientific collaboration can take place through informal discussion over a cup of coffee, but also includes more formal interactions, such as presenting at conferences and engaging in **scholarly peer review**. Scholarly peer review is the process where an author's work must pass the scrutiny of other experts in the field before being published in a journal or book. This helps keep scientists accountable for ethically responsible research projects and papers. Additionally, presenting data at conferences and in articles and books allows researchers to potentially receive critical feedback from academic peers and others to test these ideas and further the field of science toward identifying the best explanations.

Hypotheses, Theories, and Laws

Scientific investigation occurs at many levels, from investigating individual cases (for example, "What is causing this child's mysterious illness?") to understanding processes that affect most of us ("What is the ideal amount of sleep for an adult?"). All of these questions are important and will generate different types of testable scientific explanations. So far, we have used the term "hypothesis" to describe these scientific explanations for why observed phenomena are the way they are. Hypotheses are typically explanations that address a narrow set of phenomena, such as (in anthropology), a particular population or primate species.

In science, a **theory** is an explanation of observations that addresses a *wide* range of phenomena. Like hypotheses, theories also explain how or why something occurs, rely on empirical evidence, and are testable and able to be refuted. Because the term theory is often used casually outside of science, you may hear people try to dismiss a scientific claim as "just a theory." In science there are often multiple competing theories, but over time some are eliminated, leaving the theory or theories that best explain the most evidence. Scientific theories that have stood the test of time are thus supported by many lines of evidence and are usually reliable. Some well-tested theories accepted by most scientists include the theory of general relativity, which explains the law of gravitation and its relation to other forces, and evolutionary theory, which describes how heritable traits can change in a population over time.

While scientific hypotheses and theories share many characteristics, laws are quite different. A **law** is a prediction about what will happen given certain conditions, *not* an explanation for how or why it happens. A law is not a "mature" version of a theory. For example, Newton's universal law of gravity allows us to predict the gravitational force (F) between any two objects using the equation F = G(m1m2)/r2, but it does not explain *why* gravity works. Laws are often mathematical, and some well-known laws include Newton's three laws of motion and laws of genetic inheritance. Laws are important, and their discovery often promotes the development of theories.



Figure 1.1.4.5: *Archimedes is portrayed here having just discovered his Principle of Buoyancy. The vignette is by Count Giammaria Mazzuchelli (1707–1765).*

To demonstrate how important laws can be—and show how unusual things can inspire scientific discoveries—we can use the story of the ancient Greek mathematician and inventor Archimedes. Archimedes' buoyancy principle is a law that is useful for many things, including density calculations and designing ships. Purportedly, he made this discovery when he noticed the water level rise in the bathtub when he climbed in it. Realizing its importance, he is said to have shouted "Eureka" and proceeded to run naked through the city of Syracuse. While this is a fun story (that may or may not be true), it does remain that scientific laws, alongside scientific hypotheses and theories, do have a very important role in the scientific process and in generating scientific explanations about our natural world.

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1.1.5: Ways of Knowing- Science, Faith, and Anthropology

In anthropology, we recognize that there are many ways people have of knowing things. Human knowledge is very diverse. For instance, you might know that fingernails are softer than metal because as a child you accidentally stapled through your fingernail while doing an art project (a coauthor of this chapter once experienced this). This would be an example of knowledge you gained through experience. You might also know that inserting a knife into an electrical outlet is dangerous and could harm your health. Hopefully you know this not from personal experience, but through instruction from parents, teachers, and others in your social group. The degree to which humans rely on and benefit from the experiential knowledge of others is an important characteristic of what makes us human!

A unified way of knowing that is shared by a group of people and is used to explain and predict phenomena is called a **knowledge system**. Human knowledge systems are diverse and reflect the wide range of cultures and societies throughout the world and through time.

Science and religion are both knowledge systems and it is useful to understand how they differ. The type of knowledge gained from science is oftentimes called scientific **understanding**. As we have explored in the previous section, scientific understanding can change and relies on evidence and rigorous, repeated testing. Religious ways of knowing are called **belief**, which is different from scientific understanding because it does not require repeated testing or validation (although it can rely on observations and experiences). Instead, religious belief relies on trust and **faith**.

Since the beginning of the discipline, anthropologists have been interested in understanding religion because it can be important to understanding human cultures. However, religion (as well as magic, witchcraft, and other faith-based traditions) has proven notoriously difficult to define from an anthropological perspective, partly because there are so many religious practices and beliefs throughout the world that play different roles in people's lives. For instance, some religions have multiple supernatural deities or gods, such as Hinduism, while others have hardly any supernatural elements, such as Buddhism. Some have beliefs that relate to energies and powers found in certain objects, animals, and people, while others place faith in ancestors and collective cultural heritage. Some religions provide instruction on nearly every day-to-day activity a person does, while others provide merely a rough framework for how one should act and behave. Emile Durkheim (1858-1917), an early social scientist, offered a definition of religion as "a unified set of beliefs and practices relative to sacred things, that is to say, things set apart and forbidden—beliefs and practices which unite [into] one single moral community, all those who adhere to them" (Durkheim 2008).

Different individuals, cultures and societies may place more value on one type of knowing than another, although most use a combination that includes science and religion. In fact, in the early twentieth century, Bronisław Malinowski (1884-1942), an important early anthropologist, concluded that all societies use religion and science in some way or another. These are common ways that humans have of knowing our world.

In contemporary societies such as the United States, science and (some) religions conflict on the topic of human origins. Nearly every culture and society has a unique origin story that explains where they came from and how they came to be who they are today. These stories are often integrated into the culture's religious belief system. Many anthropologists are interested in faith-based origin stories and other beliefs because they show us how a particular group of people explain the world and their place in it. Anthropologists also value scientific understanding as the basis for how humans vary biologically and change over time. In other words, anthropologists value the multiple knowledge systems of different groups and use them to understand the human condition in a broad and inclusive way.

It is also important to note that scientists often depend on the local knowledge of the people they work with to help them understand elements of the natural or physical world that science has not yet investigated. Many groups, including **indigenous** peoples, know about the world through prolonged relationships with the environment. Indigenous knowledge systems—those ways of knowing about and explaining the world that are specific to an indigenous community or group—are informed by their own empirical observation of a specific environment and passed down over generations.

While religion and indigenous knowledge systems may play a complementary role in helping anthropologists understand the human condition, they are distinct from science. The anthropological subdiscipline of biological anthropology is based on scientific ways of knowing about humans and human origins. In this text we will exclusively explore what science tells us about how humans came to be and why we are the way we are today. Therefore, you do not need to *believe* in evolution to master this material, because belief is not a scientific way of knowing. For this textbook, you only need to *understand* the scientific perspective(s) of evolution.

Throughout our lives, each of us work to reconcile and integrate into our worldview the different ways we have of knowing things. This is part of our lifelong intellectual journey. It is also, in our opinion, one of the most exciting parts of learning. We are pleased you have joined us on this journey of knowledge about humanity and yourself! Welcome!

Review Questions

- What are some key approaches to anthropological research?
- How has the discipline of anthropology changed over time?
- What are some similarities and differences between the subdisciplines? How does the “fifth subdiscipline” of applied anthropology fit within the larger discipline of anthropology?
- What are some subfields of biological anthropology and what do those anthropologists study?
- What is science? What is the scientific method? How does science compare to other ways of knowing?

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1.1.6: Key Terms

Belief (religious): A firmly held opinion or conviction typically based on spiritual apprehension rather than empirical proof.

Bipedal: Habitually using only two legs to walk.

Cultural relativism: The anthropological practice of suspending judgment and seeking to understand another culture on its own terms sympathetically enough so that the culture appears to be a coherent and meaningful design for living.

Empirical: Evidence that is verifiable by observation or experience instead of relying primarily on logic or theory.

Ethnocentrism: The opinion that one's own way of life is natural or correct and the only true way of being fully human.

Faith (religious): Complete trust or confidence in the doctrines of a religion, typically based on spiritual apprehension rather than empirical proof.

Historical archaeologists: Archaeologists who excavate and analyze material remains to supplement a society's written records.

Holism: The idea that the parts of a system interconnect and interact to make up the whole.

Hominins: Species that are regarded as human, directly ancestral to humans, or very closely related to humans.

Human variation: The range of forms of any human characteristic, such as body shape or skin color.

Human adaptation: The ways in which human bodies, people, or cultures change, often in ways better suited to the environment or social context.

Hypothesis: Explanation of observed facts; explains how and why observed phenomena are the way they are. Scientific hypotheses rely on empirical evidence, are testable, and are able to be refuted.

Indigenous: Refers to people who are the original settlers of a given region and have deep ties to that place. Also known as First Peoples, Aboriginal Peoples, or Native Peoples, these populations are in contrast to other groups who have settled, occupied, or colonized the area more recently.

Knowledge system: A unified way of knowing that is shared by a group of people and is used to explain and predict phenomena.

Law: A prediction about what will happen given certain conditions; typically mathematical.

Participant observation: A research method common in cultural anthropology that involves living with, observing, and participating in the same activities as the people one studies.

Prehistoric archaeologists: Archaeologists who survey, excavate, and analyze material remains to study civilizations that lacked written records.

Sapir-Whorf hypothesis: The principle that the language you speak allows you to think about some things and not other things. This is also known as the linguistic relativity hypothesis.

Scholarly peer review: The process where an author's work must pass the scrutiny of other experts in the field before being published in a journal or book.

Subdiscipline: These refer to the four major areas that make up the discipline of anthropology: biological anthropology, cultural anthropology, archaeology, and linguistic anthropology.

Subfield: In this book, subfield refers to the different specializations within biological anthropology, including primatology, paleoanthropology, molecular anthropology, bioarchaeology, forensic anthropology, and human biology.

Theory: An explanation of observations that typically addresses a wide range of phenomena.

Understanding (scientific): Knowledge accumulated by systematic scientific study, supported by rigorous testing and organized by general principles.

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CHAPTER OVERVIEW

2: Meet the primates! - Evolution, Characteristics and Taxonomy

2.1: Meet the Living Primates

2.1.1: What is a Primate?

2.1.2: Key Traits Used to Distinguish Between Primate Taxa

2.1.3: Primate Diversity

2.1.4: Learning From Primates

2.1.5: Key Terms

2.2: Primate Evolution

2.2.1: How to Diagnose a Primate

2.2.2: Major Hypotheses About Primate Origins

2.2.3: The Origin of Primates

2.2.4: The Emergence of Modern Primate Groups

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2.2.6: Key Terms

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2.1: Meet the Living Primates

Stephanie Etting, Ph.D., Sacramento City College

Learning Objectives

- Learn how primates are different from other mammals.
- Understand how studying non-human primates is important in anthropology.
- Identify different types of traits that we use to evaluate primate taxa.
- Describe the major primate taxa using their key characteristics.
- Understand your place in nature by learning your taxonomic classification.

One of the best parts of teaching anthropology for me is getting to spend time at zoos watching primates. What I also find interesting is watching people watch primates. I have very often heard a parent and child walk up to a chimpanzee enclosure and exclaim “Look at the monkeys!” The parent and child often don’t know that a chimpanzee is not a monkey, nor are they likely to know that chimpanzees share more than 98% of their DNA with us. What strikes me as significant is that, although most people do not know the difference between a monkey, an ape, and a lemur, they nonetheless recognize something in the animals as being similar to themselves. What people probably mean when they say “monkey” is actually “primate,” a term that refers to all organisms classified within the Order Primates and also the subject of this chapter. You may be wondering why a field dedicated to the study of humans would include the study of non-human animals. Because humans are primates, we share a wide range of behavioral and morphological traits with the other species who also fall into this group. In Chapter 2, you learned about the nature of Linnaean classification, the system we use for organizing life-forms. Here, we focus on the organization and diversity within the Order Primates. The term *Order Primates* dates back to 1758 when, in his tenth edition of *SystemaNaturae*, Carolus Linnaeus put humans, “simia” (monkeys and apes), “lemurs” (lemurs and colugos), and some bats into one of eight groups of mammals. Linnaeus was wrong in including colugos (now in Order Dermoptera) and bats (now in Order Chiroptera), but the grouping of humans with the then-known non-human primates was significant in that by doing so Linnaeus formally recognized the affinities between humans and these non-human taxa. In fact, acknowledgment of similarities between humans and non-humans dates back far earlier than Linnaeus (see the Special Topic box), yet it was only more recently that we attained the genetic data to back up our intuition.

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Stephanie Etting

Dr. Stephanie Etting became hooked on biological anthropology as a freshman at UC Davis when she took the “Introduction to Biological Anthropology” course. She obtained her Ph.D. in anthropology in 2011 from UC Davis, where she studied anti-predator behavior toward snakes in rhesus macaques, squirrel monkeys, and black-and-white ruffed lemurs. While in graduate school, Dr. Etting discovered her love of teaching and, since finishing her dissertation, has taught at UC Berkeley; Sonoma State University; UC Davis; California State University, Sacramento; and Sacramento City College. In addition to her interests in primate behavior, Dr.

For Further Exploration

Animal Diversity Web: https://animaldiversity.org/accounts/Primates/specimens/ This website is hosted by the Zoology Department at the University of Michigan. It has photographs of skulls, teeth, hands, arms, and feet of many primate species.

eSkeletons: http://www.eskeletons.org This website is hosted by the Department of Anthropology at University of Texas, Austin. It is an interactive website where you can compare specific bones from different species of primates.

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2.1.1: What is a Primate?

Primates are one of at least twenty Orders belonging to the Class Mammalia. All members of this class share certain characteristics, including, among other things, having fur or hair, producing milk from mammary glands, and being warm-blooded. There are three types of mammals: monotremes, marsupials, and placental mammals. Monotremes are the most primitive of the mammals, meaning they have retained more ancient traits than marsupials or placental mammals, and so, monotremes are characterized by some unusual traits. Monotremes, which include echidnas and duck-billed platypuses, lay eggs rather than give birth to live young. Once the young hatch, they lap up milk produced from glands on the mother's abdomen rather than latch onto nipples. Marsupial mammals are those, like kangaroos and koalas, who internally gestate for a very short period of time and give birth to relatively undeveloped young. Joeys, as these newborns are called, complete their growth externally in their mother's pouch where they suckle. Lastly, there are placental mammals. Placental mammals internally gestate for a longer period of time and give birth to fairly well-developed young who are then nursed. Primates, including ourselves, belong to this last group. Among the diversity of mammalian orders alive today, primates are very likely one of the oldest. One genetic estimate puts the origin of primates at approximately 91 million years ago (mya), predating the extinction of the dinosaurs (Bininda-Emonds et al. 2007). Today, the Order Primates is a diverse group of animals that includes lemurs and lorises, tarsiers, monkeys of the New and Old Worlds, apes, and humans, all of which are united in sharing a suite of anatomical, behavioral, and life history characteristics. Before delving into the specific traits that distinguish primates from other animals, it is important to first discuss the different types of traits that we will encounter.

Types of Traits

When evaluating relationships between different groups of primates, we use key traits that allow us to determine which species are most closely related to one another. Traits can be either primitive or derived. **Primitive** traits are those that a taxon has because it has inherited the trait from a distant ancestor. For example, all primates have body hair because we are mammals and all mammals share an ancestor hundreds of millions of years ago that had body hair. This trait has been passed down to all mammals from this shared ancestor, so all mammals alive today have body hair. **Derived** traits are those that have been more recently altered. This type of trait is most useful when we are trying to distinguish one group from another because derived traits tell us which taxa are more closely related to each other. For example, humans walk on two legs. The many adaptations that humans possess which allow us to move in this way evolved after humans split from the Genus *Pan*. This means that when we find fossil taxa that share derived traits for walking on two legs, we can conclude that they are likely more closely related to humans than to chimpanzees and bonobos.

There are a couple of other important points about primitive and derived traits that will become apparent as we discuss primate diversity. First, the terms *primitive* and *derived* are relative terms. This means that depending on what taxa are being compared, a trait can be either one. For example, in the previous section, body hair was used as an example for a primitive trait among primates. All mammals have body hair because we share a distant ancestor who had this trait. The presence of body hair therefore doesn't allow you to distinguish whether monkeys are more closely related to apes or lemurs because they all share this trait. However, if we are comparing mammals to birds and fish, then body hair becomes a derived trait of mammals. It evolved after mammals diverged from birds and fish, and it tells us that all mammals are more closely related to each other than they are to birds or fish. The second important point is that very often when one lineage splits into two, one taxon will stay more similar to the last common ancestor in retaining more primitive traits, whereas the other lineage will usually become more different from the last common ancestor by developing more derived traits. This will become very apparent when we discuss the two suborders of primates, Strepsirrhini and Haplorrhini.When these two lineages diverged, strepsirrhines retained more primitive traits (those present in the ancestor of primates) and haplorrhines developed more derived traits (became more different from the ancestor of primates).

There are two other types of traits that will be relevant to our discussions here: generalized and specialized traits. **Generalized traits** are those characteristics that are useful for a wide range of things. Having **opposable thumbs** that go in a different direction than the rest of your fingers is a very useful, generalized trait. You can hold a pen, grab a branch, peel a banana, or text your friends all thanks to your opposable thumbs. **Specialized traits** are those that have been modified for a specific purpose. These traits may not have a wide range of uses, but they will be very efficient at their job. Hooves in horses are a good example of a specialized trait. Horses cannot grasp objects with their hooves, but hooves allow horses to run very quickly on the ground on all fours. You can think of generalized traits as a Swiss Army knife, useful for a wide range of tasks but not particularly good at any of one them. That is, if you're in a bind, then a Swiss Army knife can be very useful to cut a rope or fix a loose screw, but if you were going to build furniture or fix a kitchen sink, then you'd want specialized tools for the job. As we will see, most primate traits tend to be generalized.

Primate Suite of Traits

The Order Primates is distinguished from other groups of mammals in having a suite of characteristics. This means that there is no individual trait that you can use to instantly identify an animal as a primate; instead, you have to look for animals that possess a collection of traits. What this also means is that each individual trait we discuss may be found in non-primates, but if you see an animal that has most or all of these traits, there is a good chance it is a primate.

One area in which the Order Primates is most distinguished from other organisms regards traits related to our senses, especially our vision. Compared to other animals, primates rely on vision as a primary sense. Our heavy reliance on vision is reflected in many areas of our anatomy and behavior. All primates have eyes that face forward with convergent (overlapping) visual fields. This means that if you cover one eye with your hand, you can still see most of the room with your other one. This also means that we cannot see on the sides or behind us as well as some other animals can. In order to protect the sides of the eyes from the muscles we use for chewing, all primates have at least a **postorbital bar,** a bony ring around the outside of the eye (Figure 5.1). Some primate taxa have more convergent eyes than others, so those primates need extra protection for their eyes. As a result, animals with greater orbital convergence will have a **postorbital plate** or**postorbital closure** in addition to the bar (Figure 5.1). The postorbital bar is a derived trait of primates, appearing in our earliest ancestors, which you will read more about in Chapter 8.

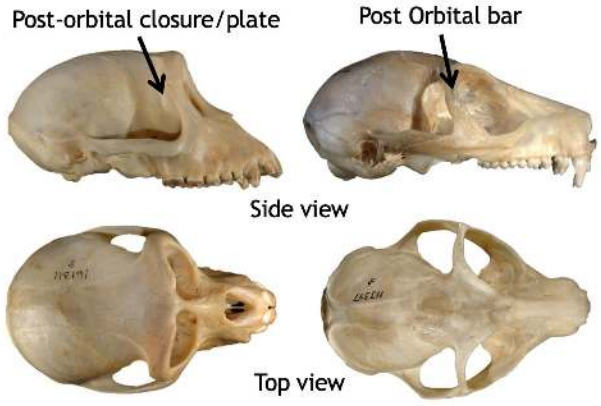


Figure 2.1.1.1: All primates have some form of bony protection around their eyes. Some have a postorbital bar only (right), but many have full postorbital closure, also called a postorbital plate, that completely protects the back of the eye socket (left).

Another important and distinctive trait of our Order is that many primates have **trichromatic color vision**, the ability to distinguish reds and yellows in addition to blues and greens. Interestingly, birds, fish, and reptiles are **tetrachromatic** (they can see reds, yellows, blues, greens, and even ultraviolet), but most mammals, including some primates, are only **dichromatic** (they see only in blues and greens). It is thought that the nocturnal ancestors of mammals benefited from seeing better at night rather than in color, and so dichromacy is thought to be the primitive condition for mammals. There is a lot of interest in why some primates would re-evolve trichromacy. Some theories revolve around food, arguing that the ability to see reds/yellows may allow primates who can see these colors to better detect young leaves (Dominy and Lucas 2001) or ripe fruits (Regan et al. 2001) against an otherwise green, leafy background. Color vision has also been suggested to be useful for detecting predators, especially big cats (Pessoa et al. 2014). Another theory emphasizes the usefulness of trichromacy in social and mate-choice contexts (Changizi et al. 2006). Thus far there is no consensus, as trichromatic color vision can be useful in many circumstances. There is also the added complication that sometimes dichromacy is more advantageous, as animals who are dichromatic are usually better at seeing through camouflage to find hidden items like foods or predators (Morgan et al. 1992). Therefore, investigating the evolution of color vision continues to be an interesting and ongoing area of research.

Primates also differ from other mammals in the size and complexity of our brains. All primates have brains that are larger than you would expect when compared to other mammals of the same size. On average, primates have brains that are twice as big for their body size as you would expect when compared to other mammals. Not unexpectedly, the visual centers of the brain are larger in primates and the wiring is different from that in other animals, reflecting our reliance on this sense. The neocortex, which is used for higher functions like consciousness and language in humans, as well as sensory perception and spatial awareness, is also larger in primates relative to other animals. In non-primates this part of the brain is often smooth, but in primates it is made up of many folds which increase the surface area. It has been proposed that the more complex neocortex of primates is related to diet, with fruit-eating primates having larger relative brain sizes than leaf-eating primates, due to the more challenging cognitive demands required to find and process fruits (Clutton-Brock and Harvey 1980). An alternative hypothesis argues that larger brain size is

necessary for navigating the complexities of primate social life, with larger brains occurring in species who live in larger, more complex groups relative to those living in pairs or solitarily (Dunbar 1998). There seems to be support for both hypotheses, as large brains are a benefit under both sets of selective pressures.

The primate visual system uses a lot of energy, so primates have compensated by cutting back on other sensory systems, particularly our sense of smell. Compared to other mammals, primates have relatively reduced snouts. This is another derived trait of primates that appears even in our earliest ancestors. As we will discuss, there is variation across primate taxa in how much snouts are reduced. Those with a better sense of smell usually have poorer vision than those with a relatively dull sense of smell. The reason for this is that all organisms have a limited amount of energy to spend on running our bodies, so we make evolutionary trade-offs, because energy spent on one trait must mean cutting back on energy spent on another. With regards to primate senses, primates with better vision (more convergent eyes, better visual acuity, etc.) are spending more energy on vision and thus will have poorer smell (and a shorter snout). Primates who spend less energy on vision (less convergent eyes, poorer visual acuity, etc.) will have a better sense of smell (and a longer snout).



Figure 2.1.1.2: These drawings of the hands and feet of different primates clearly show the opposable thumbs and big toes, pentadactyly, flattened nails, and tactile pads that are characteristic of our Order.

Primates also differ from other animals in our hands and feet. The Order Primates is a largely **arboreal** taxonomic group, which means that most primates spend a significant amount of their time in trees. As a result, the hands and feet of primates have evolved to move around in a three-dimensional environment. Primates have the generalized trait of **pentadactyly**— possessing five digits (fingers and toes) on each limb. Many non-primates, like dogs and horses, have fewer digits because they are specialized for high-speed, **terrestrial** (on the ground) running. Pentadactyly is also a primitive trait, one that dates back to the earliest four-footed animals. Primates today have opposable thumbs and, except humans, opposable big toes (Figure 5.2). Opposable thumbs/toes are a derived trait that appeared in the earliest primates about 55 million years ago. Having thumbs and big toes that go in a different direction from the rest of the fingers and toes allow primates to be excellent climbers in trees but also allow us to manipulate objects. Our ability to manipulate objects is further enhanced by the flattened nails on the backs of our fingers and toes that we possess in the place of the claws and hooves that many other mammals have. On the other side of our digits, we have sensitive **tactile pads** that allow us to have a fine sense of touch. Primates use this fine sense of touch for handling food and, in many species, grooming themselves and others. In primates, grooming is an important social currency, through which individuals forge and maintain social bonds. You will learn more about grooming in Chapter 6.

Animals with large brains usually have extended life history patterns, and primates are no exception. **Life history** refers to the pace at which an organism grows, reproduces, ages, and so forth. Some animals grow very quickly and reproduce many offspring in a short time frame, but do not live very long. Other animals grow slowly, reproduce few offspring, reproduce infrequently, and live a long time. Primates are all in the “slow lane” of life history patterns. Compared to animals of similar body size, primates grow and develop more slowly, have fewer offspring per pregnancy, reproduce less often, and live longer. Primates also invest heavily in each offspring, a subject you will learn more about in the next chapter. With a few exceptions, most primates only have one offspring at a time. There is a group of small-bodied monkeys in the New World who regularly give birth to twins, and some lemurs are able to give birth to multiple offspring at a time, but these primates are the exception rather than the rule. Primates also reproduce relatively infrequently. The fastest-reproducing primates will produce offspring about every six months, while the slowest, the orangutan, reproduces only once every seven to nine years. This very slow reproductive rate makes the orangutan the slowest-reproducing animal on the planet! Primates are also characterized by having long lifespans. The group that includes

humans and large-bodied apes has the most extended life history patterns among all primates, with some large-bodied apes estimated to live up to 58 years in the wild (Robson et al. 2006).

Lastly, primates share some behavioral and ecological traits. Primates are very social animals, and all primates, even those that search for food alone, have strong social networks with others of their species. Indeed, social networks in primates have been shown to be crucial in times of stress and to enhance reproductive success (Silk et al. 2009). Unlike many animals, primates do not migrate. This means that primates stay in a relatively stable area for their whole life, often interacting with the same individuals for their long lives. The long-term relationships that primates form with others of their species lead to complex and fascinating social behaviors, which you will read about in Chapter 6. Finally, non-human primates show a clear preference for tropical regions of the world. Most primates are found between the Tropic of Cancer and the Tropic of Capricorn, with only a few taxa living outside of these regions. You can see a summary of the primate suite of traits in Figure 5.3.

Table 5.1.1: Primate Traits at a Glance: This table summarizes the suite of traits that differentiate primates from other mammals

Primate suite of traits
Convergent eyes
Post-orbital bar
Many have trichromatic color vision
Short snouts
Opposable thumbs and big toes
Pentadactyly
Flattened nails
Tactile pads
Highly arboreal
Large brains
Extended life histories
Live in the tropics

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2.1.2: Key Traits Used to Distinguish Between Primate Taxa

When trying to place primate species into specific taxonomic groups, we use a variety of dental characteristics, locomotor adaptations, and behavioral adaptations. Differences in these characteristics across groups reflect constraints of evolutionary history as well as variation in adaptations.

Dental Characteristics

Teeth may not seem like the most exciting topic with which to start, but we can learn a tremendous amount of information about an organism from its teeth. First, teeth are vital to survival. Wild animals do not have the benefit of knives and forks, and so rely primarily on their teeth to process their food. Because of this, teeth of any species have evolved to reflect what that organism eats and so tell us directly about their diet. Second, variation in tooth size, shape, and number tells us a lot about an organism's evolutionary history. Some taxa have more teeth than others or different forms of teeth than others. Furthermore, differences in teeth between males and females can tell us about competition over mates (see Chapter 6). Lastly, teeth preserve really well in the fossil record. Enamel is hard, and there is little meat on jaws so carnivores and scavengers often leave them behind. Because of this, very often we find a lot of fossil jaws and teeth, and so we need to be able to learn as much as we can from those pieces.

Figure 2.1.2.1: This open-mouthed Hamadryas baboon clearly demonstrates the diastema between his upper canine and front teeth. This space is taken up by his lower canine when he closes his mouth.

If you've ever seen the jaws of a shark, dinosaur, or crocodile, you were probably struck by how sharp their teeth were and by the sheer number of teeth they had. What you probably didn't think about was that they also only have one type of tooth, referred to as **homodont.** In fact, one of the ways that mammals differ from other organisms is that we have multiple types of teeth (**heterodont**) that we use in different ways. We have **incisors**, which we use for slicing; we have **premolars** and **molars**, which we use for grinding up our food; and we have **canines**, which most primates (not humans) use as weapons against predators and each other. The sizes of canines vary across species and can often be **sexually dimorphic**, with male canines usually being larger than those of females. Non-human primates often **hone**, or sharpen, their canines by gnashing the teeth together to sharpen the sides. The upper canine sharpens on the first lower premolar and the lower canine sharpens on the front of the upper canine. As canines get larger, they require a space to fit in order for the jaws to close. This space between the teeth is called a **diastema** (Figure 5.4).

Figure 2.1.2.2: This drawing shows half of the human mandible. With the four types of teeth labeled, you can determine that the dental formula is 2:1:2:3.

As discussed before, primate taxa can vary in the numbers and forms of teeth they have. We determine the number of each type of tooth an organism has by its **dental formula**. The dental formula tells you how many incisors, canines, premolars, and molars are in each quadrant of the mouth (half of the top or bottom). For example, Figure 5.5 shows half of the lower teeth of a human. You

can see that in half of the mandible, there are two incisors, one canine, two premolars, and three molars. This dental formula is written as 2:1:2:3. (The first number represents the number of incisors, followed by the number of canines, premolars, and molars). Some early fossil primates had a dental formula of 2:1:4:3, but among the living primates, none have more teeth than can be found in a 2:1:3:3 dental formula. Many have fewer teeth, however, and some have a different dental formula on the top than they do on the bottom.

To determine the dental formula, you need to be able to identify the different types of teeth. You can recognize incisors because they often look like spatulas with a flat, blade-like surface. Premolars and molars can be differentiated by the number of **cusps** that they have. Cusps are the little bumps (which in some species can be quite sharp) that you can feel with your tongue on the surface of your back teeth. Premolars are smaller than molars and, in primates, often have one or two cusps on them. Molars are bigger, with a larger chewing surface, and so have more cusps. Depending on the species of primate and whether you're looking at upper or lower teeth, molars can have between three and five cusps. There is even one extinct primate (*Oreopithecus*) who had six cusps on its molars. Molar cusps can also vary between taxa in how they are arranged, as you will learn more about later in this chapter. Canines are often easy to distinguish because they are usually much longer and more conical than the other teeth. This is not always the case, however, as you will see when you read about the teeth of lemurs and lorises.

Teeth also tell us directly about an organism's diet. Primates are known to eat a wide range of plant parts, insects, gums, and, rarely, meat. While all primates eat a variety of foods, what differs among primates are the proportions of each of these food items in the diet. That is, two primates living in the same forest may be eating the same foods but in vastly different proportions, and so we would categorize them as different dietary types. The most common dietary types among primates are those whose diets consist primarily of fruit (**frugivores**), those who eat mostly insects (**insectivores**), and those who eat primarily leaves (**folivores**). Fewer primates are **gummivores**, who specialize in eating gums and saps, so we will not discuss the adaptations for this dietary type in great detail.

Frugivores

Plants want animals to eat their fruits because, in doing so, animals eat the seeds of the fruit and then disperse them far away from the parent plant. Because plants want animals to eat the fruit, plants often "advertise" fruits by making them colorful and easy to spot, full of easy-to-digest sugars that make them taste good—and, often, easy to chew and digest (not being too fibrous or tough). For these reasons, frugivores often do not need a lot of specialized traits to consume a diet rich in fruits (Figure 5.6a). Their molars usually have a broad chewing surface with low, rounded cusps (referred to as **bunodont** molars). Frugivores also often have large incisors for slicing through the outer coatings on fruit. Primates that eat fruit tend to have stomachs, colons, and small intestines that are intermediate in terms of size and complexity between insectivores and folivores (Chivers and Hladik 1980). They are also usually of intermediate body size between the other two dietary types. Because fruit does not contain protein, frugivores must supplement their diet with protein from insects and/or leaves. Some frugivorous primates get protein by eating seeds and so have evolved to have thicker enamel on their teeth to protect them from excessive wear.

Table 5.2.1: Frugivores are characterized by large incisors, bunodont molars, and digestive tracts that are intermediate in complexity between the other two dietary types.

Large incisors	**Bunodont molars**	**Intermediate complexity of digestive tract**

Insectivores

Insects can be difficult to find and catch but are not typically difficult to chew. As a result, insectivorous primates usually have small molars with pointed cusps that allow them to puncture the exoskeleton of the insects (Figure 5.6b). Once the outer shells of the insects are punctured, insects are not difficult to digest, so insectivores have simple stomachs and colons and a long small intestine. Nutritionally, insects provide a lot of protein and fat but are not plentiful enough in the environment to support large-bodied animals, so insectivores are usually the smallest of the primates.

Table 5.2.2: Insectivores need sharp, pointed molar cusps in order to break through the exoskeletons of insects. Insects are easy to digest, so these primates have simple digestive tracts.

Sharp, pointed molars	**Simple digestive tract**

Folivores

Unlike with fruits, plants do not want animals to eat their leaves. Leaves are the way plants get their energy from the sun, therefore, plants evolved to make their leaves very difficult for animals to eat. Leaves often have toxins in them, taste bitter, are very fibrous and difficult to chew, and are made of large cellulose molecules that are difficult to break down into usable sugars. Because of these defenses, animals who eat leaves need a lot of specialized traits (Figure 5.6c). Folivorous primates have broad molars with high, sharp cusps connected by **shearing crests**. These molar traits allow folivores to physically break down fibrous leaves when chewing. Folivores then have to chemically break down cellulose molecules into usable energy, so these animals need specialized digestive systems. Some folivores have complex stomachs with multiple compartments, but all leaf eaters have large, long intestines and special gut bacteria that can break up cellulose. Folivores are usually the largest bodied of all primates, and they spend a large portion of their day digesting their food, so they are often less active than frugivores or insectivores.

Table 5.2.3: In order to derive energy from leaves, folivores have smaller incisors, high, sharp molar cusps connected by shearing crests and complex digestive tracts filled with specialized bacteria.

Smaller incisors	**High, sharp molar cusps with shearing crests**	**Complex digestive tract**

Behavioral Adaptations

Chapter 6 is entirely dedicated to primate behavior, so only broad differences related to taxonomic classification will be discussed here. These differences include variations in activity patterns, social grouping, and habitat use. Primate groups often differ in **activity patterns**—that is, whether they are active during the day (**diurnal**), at night (**nocturnal**), or through the 24-hour period (**cathemeral**). We also see variations among primate groups in social groupings: some taxa are primarily solitary, others live in pairs, and still others live in groups of varying sizes and compositions. Lastly, some taxa are primarily arboreal while others are more terrestrial.

Locomotor Adaptations

Figure 2.1.2.3: An example of a vertical clinger and leaper. Note the longer legs than arms, long lower back and long fingers and toes. This vertical clinger and leaper doesn't have a tail, but most have long tails as well.

Finally, primate groups vary in their adaptations for different forms of **locomotion**, or how they move around. Living primates are known to move by vertical clinging and leaping, quadrupedalism, brachiation, and bipedalism. **Vertical clinging and leaping** is when an animal grasps a vertical branch with its body upright, pushes off with long hind legs and then lands on another vertical support branch (Figure 5.7). Animals who move in this way usually have longer legs than arms, long fingers and toes, and smaller

bodies. Vertical clinger leapers also tend to have elongated ankle bones, which serve as a lever to help them push off with their legs and leap to another branch.

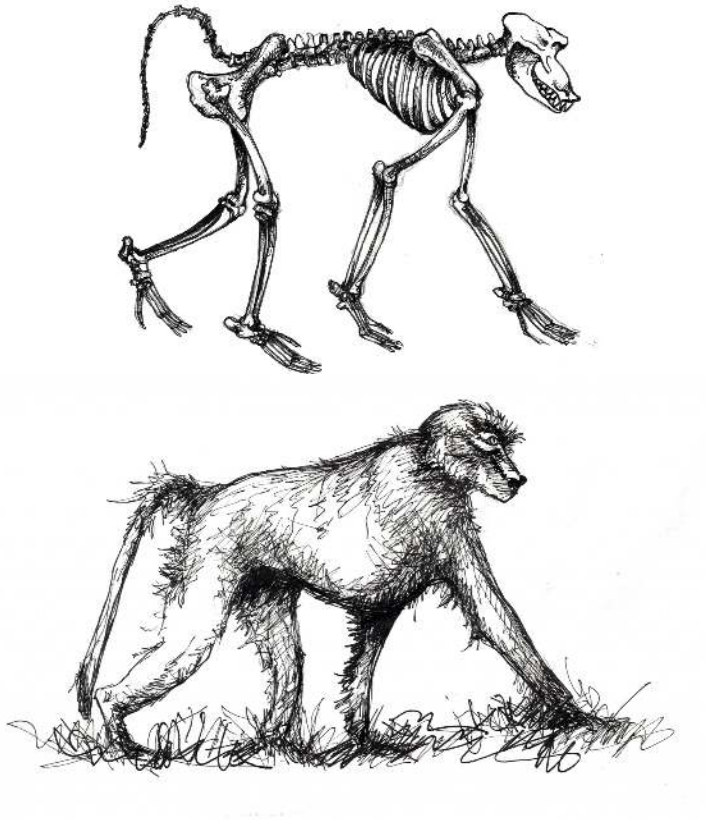


Figure 2.1.2.4: Here are examples of a typical quadrupedal primate. Note that the arms and legs are about the same length and the back is long and flexible. This is a terrestrial quadruped so the arms and legs are relatively long and the tail is shorter.

Quadrupedalism is the most common form of locomotion among primates (Figure 5.8). The term *quadrupedal* means to walk on all fours. Animals that move in this way usually have legs and arms that are about the same length and typically have a tail for balance. Arboreal quadrupeds usually have shorter arms and legs and longer tails, while terrestrial quadrupeds have longer arms and legs and, often, shorter tails. These differences relate to the lower center of gravity needed by arboreal quadrupeds for balance in trees and the longer tail required for better balance when moving along the tops of branches. Terrestrial quadrupeds have longer limbs to help them cover more distance more efficiently. You will learn more specific anatomical features of quadrupedalism later in the chapter.

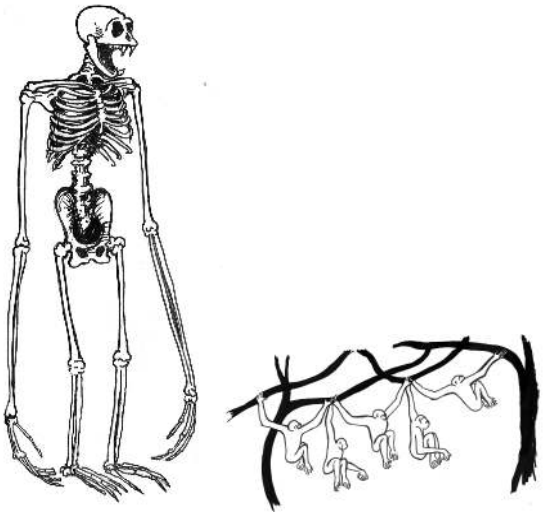


Figure 2.1.2.5: These are examples of a typical brachiator. Note the longer arms than legs, short back, and lack of a tail. You will read about more details of their anatomy later in the chapter.

Figure 2.1.2.6: Spider monkeys, like the one shown here, are considered semi-brachiators who can swing below branches but use their tails as a third limb. On the ground they move via quadrupedal locomotion.

The third form of locomotion seen in primates is **brachiation**, the way of moving you used if you played on "monkey bars" as a child. Brachiation involves swinging below branches by the hands (Figure 5.9). To be an efficient brachiator, a primate needs to have longer arms than legs, flexible shoulders and wrists, a short lower back, and no tail. You will learn more about the specifics of these traits when you learn about apes later in this chapter. Some primates move via semi-brachiation. These taxa also swing below branches but do not have all of the same specializations as brachiators. They have flexible shoulders, but their arms and legs are about the same length, useful because they are quadrupedal when on the ground. Semi-brachiators also use long **prehensile tails** as a third limb when swinging (Figure 5.10). The underside of the tail has a tactile pad, resembling your fingerprints, for better grip.

Lastly, humans move around on two feet, called **bipedalism**. Some primates will occasionally travel on two feet but do so awkwardly and never for long distances. Among mammals, only humans have evolved to walk with a striding gait on two legs as a primary form of locomotion. To move bipedally, humans need many specialized adaptations that will be discussed in detail in later chapters.

2.1.2: Key Traits Used to Distinguish Between Primate Taxa is shared under a not declared license and was authored, remixed, and/or curated by LibreTexts.

2.1.3: Primate Diversity

As we begin exploring the different taxa of primates, it is important to keep in mind the hierarchical nature of taxonomic classification (discussed in Chapter 2) and how this relates to the key characteristics that will be covered. Figure 5.11 summarizes the major taxonomic groups of primates. If you locate humans on the chart, you can trace our classification and see all of the categories getting more and more inclusive as you work your way up to the Order Primates. What this means is that humans will have the key traits of each of those groups. It is a good idea to refer to the figure to orient yourself as we discuss each taxon.

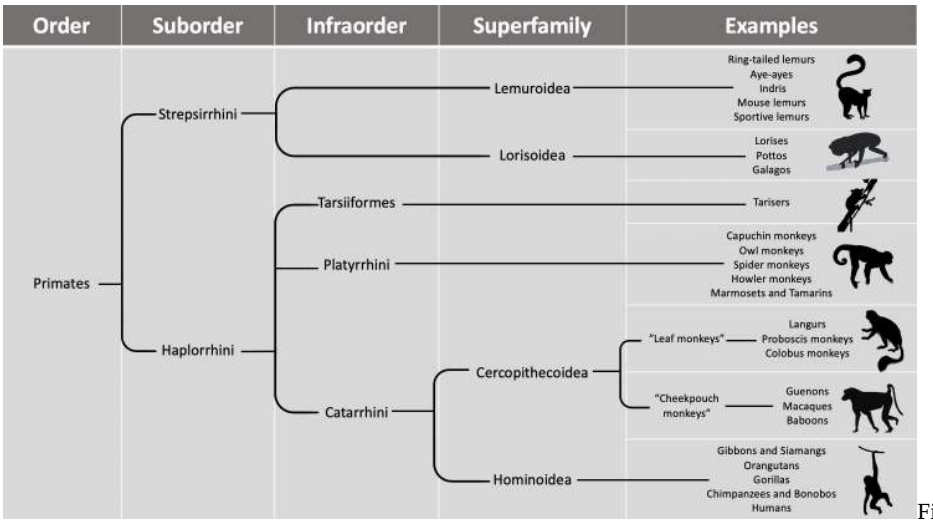


Figure 2.1.3.1: This taxonomy chart shows the major groups of primate taxa. Be sure to refer back to this chart as you read through the primate groups so that you can see how each group is related to one another.

Ways of Organizing Taxa

Our goal in taxonomic classification is to place taxa into categories that reflect their clade relationships. A **clade** is a grouping of organisms that reflect a branch of the evolutionary tree, a grouping based on relatedness. Clade relationships are determined using derived traits shared by groups of taxa as well as genetic similarities. An example of a clade would be a grouping that includes humans, chimpanzees, bonobos, and gorillas. These taxa are in what is referred to as the **African clade** of hominoids. The African clade grouping reflects the fact that humans, chimpanzees, bonobos, and gorillas all share a more recent ancestor with each other than any of them do with other species—that is, we are on the same branch of the evolutionary tree.We know members of the African clade are most closely related based on derived morphological traits as well as genetic similarities. In this grouping, we exclude the orangutan, which is considered a member of the **Asian clade** of hominoids.

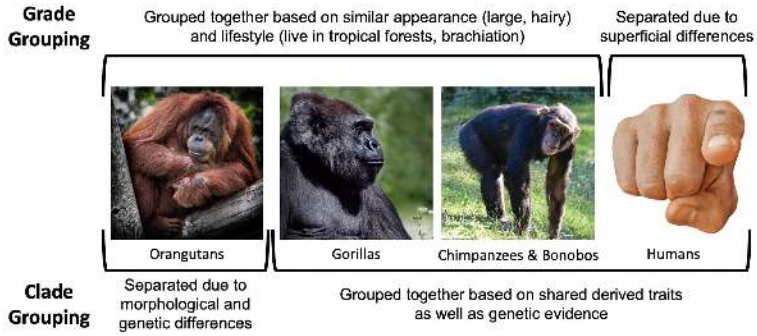


Figure 2.1.3.2: Grades vs. Clades: Grouping orangutans, gorillas, chimpanzees and bonobos but excluding humans is a grade classification based on overall similarity in appearance and lifestyle among the apes. We are most interested in groupings based on evolutionary relationships, so we use the clade classification in which humans are grouped with gorillas, chimpanzees, and bonobos. This grouping reflects our evolutionary relationships.

In contrast, **grades** are groupings that reflect levels of adaptation or overall similarity and not necessarily actual evolutionary relationships. An example of a grade would be placing orangutans, gorillas, bonobos, and chimpanzees into a group, and excluding humans. Grouping in this way is based on the superficial similarities of the apes in being large-bodied, having lots of body hair, living in tropical forests, using trees, and so on. According to these criteria, humans seem to be the unusual ones in that we differ in

our morphology, behavior, and ecology. Separating humans from the other large-bodied apes is the system that was used historically. We now know that grouping orangutans, gorillas, bonobos, and chimpanzees and excluding humans does not accurately reflect our true evolutionary relationships (Figure 5.12), and because our goal in taxonomic classification is to organize animals to reflect their evolutionary relationships, we prefer to use clade classifications.

Suborder Strepsirrhini



Figure 2.1.3.3: The foot of a ring-tailed lemur showing its grooming claw on the second digit.

The Order Primates is subdivided into Suborder Strepsirrhini and Suborder Haplorrhini, which, according to molecular estimates, split about 70–80 million years ago (Pozzi et al. 2014). The strepsirrhines include the groups commonly called lemurs, lorises, and galagos (Figure 5.14). Strepsirrhines differ from haplorrhines in many ways, most of which involve retaining primitive traits from the last common ancestor of primates. All of the traits discussed below are primitive traits, but strepsirrhines do have two key derived traits that evolved after they diverged from the haplorrhines. The two derived traits are the **grooming claw** (Figure 5.13), which is on the second digit of each foot, and the **tooth comb** (or **dental comb**), located on the lower, front teeth (Figure 5.15). In most strepsirrhines, there are six teeth in the toothcomb—the four incisors and the two canines. Other than the tooth comb, the teeth of strepsirrhines are fairly simple in not being particularly large or distinctive relative to haplorrhines.



Figure 2.1.3.4: (Clockwise from top right) sifaka, black-and-white ruffed lemur, loris, galago, slender loris, mouse lemur, aye-aye, and ring-tailed lemur.

Compared to haplorrhines, strepsirrhines rely more on nonvisual senses. Strepsirrhines have longer snouts than haplorrhines and get their name because they all have wet noses (**rhinariums**) like cats and dogs. The long snout and rhinarium reflect strepsirrhines' greater reliance on olfaction relative to haplorrhines. Indeed, many strepsirrhines use **scent marking**, rubbing scent glands or urine on objects in the environment to communicate with others. Additionally, many strepsirrhines have mobile ears that they use to locate insect prey and predators. As discussed earlier, there are trade-offs in sensory systems, so while strepsirrhines have a better sense of smell than haplorrhines, their visual adaptations are more primitive. Strepsirrhines have less convergent eyes than haplorrhines, and therefore all have postorbital bars whereas haplorrhines have full postorbital closure (Figure 5.1). All strepsirrhines have a **tapetum lucidum**, a reflective layer at the back of the eye that reflects light and thereby enhances the ability to see in low-light conditions. It is the same layer that causes your dog or cat to have "yellow eye" when you take photos of them with the flash on. It is thought to be primitive among mammals as a whole.

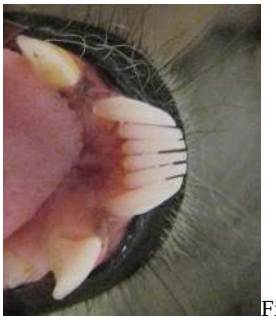


Figure 2.1.3.5: The lower front teeth of a ring-tailed lemur showing a tooth comb. Note that there are six teeth in the tooth comb, four incisors and two canines. The teeth that superficially look like canines are actually premolars.

Strepsirrhines also differ from haplorrhines in some aspects of their ecology and behavior. The majority of strepsirrhines are solitary, traveling alone to search for food, although some taxa are more social. Most strepsirrhines are also nocturnal and arboreal. Strepsirrhines are, on average, smaller than haplorrhines, and so many more of them have a diet consisting of insects and fruit, with few taxa eating primarily leaves. Lastly, most strepsirrhines are good at leaping, with several taxa specialized for vertical clinging and leaping. In fact, among primates, all but one of the vertical clinger leapers are in the Suborder Strepsirrhini.



Figure 2.1.3.6: Geographic distribution of living strepsirrhines. Lemurs live only on the island of Madagascar, while their relatives the lorises and galagos live across Central Africa and South and Southeast Asia.

Strepsirrhines can be found all across the Old World: in Asia, Africa, and on the island of Madagascar (Figure 5.16). The Suborder Strepsirrhini is divided into two groups: (1) the lemurs of Madagascar and (2) the lorises, pottos, and galagos of Africa and Asia. By molecular estimates, these two groups split about 65 million years ago (Pozzi et al. 2014).

Lemurs of Madagascar

Madagascar is an island off the east coast of Africa, and it is roughly the size of California, Oregon, and Washington combined. It has been separated from Africa for about 130 million years and from India for about 85 million years, which means it was already an island when strepsirrhines got there approximately 60–70 million years ago. Only a few mammal species ever reached Madagascar, and so when lemurs arrived they were able to flourish into a variety of forms.



Figure 2.1.3.7: Indris, the largest of the lemurs. These folivorous lemurs are vertical clingers and leapers and live in pairs.

The lemurs of Madagascar are much more diverse compared to their mainland counterparts, the lorises and galagos. Malagasy strepsirrhines display a variety of activity patterns. While many species are nocturnal, plenty of others are diurnal or cathemeral. They range in body size from the smallest of all primates, the mouse lemur, some species of which weigh a little over an ounce (Figure 5.14), up to the largest of all strepsirrhines, the indri, which weighs up to about 20 pounds (Figure 5.17). Lemurs include species that are insectivorous, frugivorous, and folivorous. A couple of members of this group have specialized in more unusual diets for primates. These include the gummivorous fork-marked lemurs as well as bamboo lemurs, who are able to metabolize the cyanide in bamboo. The most unusual lemur is the aye-aye, which you can see depicted in Figure 5.14. This nocturnal lemur exhibits traits not seen in any other primate, including having rodent-like front teeth that grow continuously and a long-bony middle finger that it uses to fish grubs out of wood. It has a very large brain compared to other strepsirrhines, which it fuels with a diet that includes bird's eggs and other animal matter. Based on genetic estimates and morphological studies, it is believed that aye-ayes were the first lemurs to separate from all of the other strepsirrhines and so have been evolving on their own since around the time strepsirrhines got to Madagascar (Matsui et al. 2009).

Lemurs are also diverse in terms of behavior. Many Malagasy strepsirrhines are solitary foragers, but some live in pairs, others in small groups, some in larger groups, and some, like the red-ruffed lemur, are now known to live in complex social groups that are unlike what we see in any other primates (Vasey 2006). It is also among the lemurs that we see some of the best vertical clingers and leapers. Many lemurs are quadrupedal, but even the quadrupedal lemurs are quite adept at leaping. Malagasy strepsirrhines also exhibit a few unusual traits. They are highly seasonal breeders, often mating only during a short window, once a year (Wright 1999). Female ring-tailed lemurs, for example, only come into estrus one day a year for a mere six hours. Malagasy strepsirrhines are also unusual in that females are socially dominant. In most primates, males dominate females because they are typically larger and exhibit greater aggression, but in lemur groups, males and females are usually the same size and females have priority access to resources over males.

Lorises, Pottos, and Galagos of Asia and Africa

Unlike the lemurs of Madagascar, lorises, pottos, and galagos live in areas where they share their environments with monkeys and apes, who often eat similar foods. Lorises live across South and Southeast Asia, while pottos and galagos live across Central Africa. Because of competition with larger-bodied monkeys and apes, mainland strepsirrhines are more restricted in the niches they can fill in their environments and so are not as diverse as the lemurs of Madagascar.



Figure 2.1.3.8: This slow loris, like all others in this taxonomic group, is solitary and nocturnal, with a diet heavy in insects and fruit.

All strepsirrhines in Africa and Asia are nocturnal and solitary. Their body sizes don't range as greatly as the lemurs, and neither do their diets. For the most part, the diet of lorises, pottos, and galagos consist of fruits and insects. A couple of species eat more gum, but overall the diet of this group is fairly narrow when compared to the Malagasy lemurs. Lorises and pottos are known for being slow, quadrupedal climbers, moving quietly through the forests to avoid being detected by predators (Figure 5.18). Because they are not fast moving, these strepsirrhines have developed alternative defenses against predators. Lorises, for example, eat a lot of caterpillars, which makes their saliva slightly toxic. Loris mothers will then bathe their young in this toxic saliva, thus making the babies unappealing to predators. In comparison to the slow-moving lorises and pottos, galagos are active quadrupedal runners and leapers that scurry about the forests at night. Galagos make distinctive calls that sound like a baby crying, which has led to their nickname "bushbabies." Figure 5.19 summarizes the key differences between these two groups of strepsirrhines.

Table 5.3.1: Strepsirrhini at a glance: This table summarizes the key differences between the two groups of strepsirrhines.

	 **Lemurs**	 **Lorises, Pottos and Galagos**
Geographic range	Madagascar	South and Southeast Asia and Central Asia
Activity patterns	Diurnal, nocturnal or cathemeral	Nocturnal
Dietary types	Insectivore, frugivore or folivore	Insectivore, frugivore
Social groupings	Solitary, pairs, or small to large groups	Solitary
Forms of locomotion	Vertical clinger leapers, quadrupedal	Slow quadrupedal climbers and active quadrupedal runners

Suborder Haplorrhini

When the strepsirrhini and haplorrhini split from one another, strepsirrhines retained more primitive traits (those likely present in the last common ancestor), while haplorrhines became quite different, developing many derived traits. Thus, all of the traits discussed below are considered derived traits.

As mentioned earlier, the visual systems of haplorrhines are more developed than those of strepsirrhines. Many haplorrhines are trichromatic and, with one exception that will be discussed shortly, all have full postorbital closure (Figure 5.1). This increase in bony closure around the eye protects the more convergent eyes that haplorrhines possess. Haplorrhines also evolved to have a **fovea**, a depression in the retina at the back of the eye containing concentrations of cells that allow us to see things very close up in great detail. The heavier reliance on vision over olfaction is also reflected in the shorter snouts ending with the **dry nose** (no rhinarium) of haplorrhines. All but two genera of living haplorrhines are active during the day, so this group lacks the tapetum lucidum which is so useful to nocturnal species. On average, haplorrhines also have larger brains relative to their body size when compared with strepsirrhines.

The Haplorrhini differ from the Strepsirrhini in aspects of ecology and behavior as well. Haplorrhines are generally larger than strepsirrhines, and so we see many more species that are folivorous and frugivorous, and fewer that are insectivorous. This dietary difference is reflected in the teeth of haplorrhines, which are broader with more surface area for chewing. The larger body size of this taxon also influences locomotion. Only one haplorrhine is a vertical clinger and leaper. Most members of this suborder are quadrupedal, with one subgroup specialized for brachiation. A few haplorrhine taxa are **monomorphic**, meaning males and females are the same size, but many members of this group show moderate to high sexual dimorphism in body size and canine size. Haplorrhines also differ in social behavior. All but two haplorrhines live in groups, which is very different from the primarily solitary strepsirrhines. Differences between the two suborders are summarized in Figure 5.20.

Table 5.3.2: Suborders at a glance: This table summarizes the key differences between the two primate suborders.

	 **Suborder Strepsirrhini**	 **Suborder Haplorrhini**
Sensory adaptations	Rhinarium Longer snout Eyes less convergent Post-orbital bar Tapetum lucidum Mobile ears	No rhinarium Short snout Eyes more convergent Post-orbital plate No tapetum lucidum Many are trichromatic Fovea
Dietary differences	Mostly insectivores and frugivores, few folivores	Few insectivores, mostly frugivores and folivores
Activity patterns and Ecology	Mostly nocturnal, few diurnal or cathemeral Almost entirely arboreal	Only two are nocturnal, rest are diurnal Many arboreal taxa, also many terrestrial taxa
Social groupings	Mostly solitary, some pairs, small to large groups	Only two are solitary, all others live in pairs, small to very large groups
Sexual dimorphism	Minimal to none	Few taxa have little/none, many taxa show moderate to high dimorphism

Suborder Haplorrhini is divided into three infraorders: Tarsiiformes, which includes the tarsiers of Asia; Platyrrhini, which includes the New World monkeys of Central and South America; and Catarrhini, a group that includes the Old World monkeys and apes of Asia and Africa, as well as humans. According to molecular estimates, tarsiers split from the other haplorrhines close to 70 million years ago, and platyrrhini split from catarrhini close to 46 million years ago (Pozzi et al. 2014).

Infraorder Tarsiiformes of Asia



Figure 2.1.3.9: Tarsiers are the only living representatives of this Infraorder.

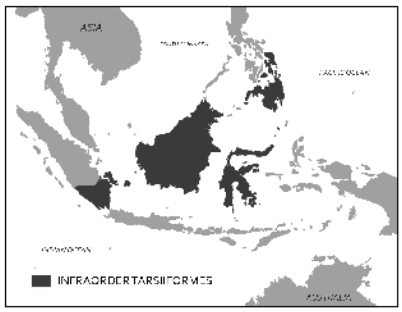


Figure 2.1.3.10: Tarsiiformes can be found in tropical forests of Southeast Asia.

Today, the Infraorder Tarsiiformes includes only one genus, Tarsius (Figure 5.21). Tarsiers are small-bodied primates that live in Southeast Asian forests (Figure 5.22) and possess an unusual collection of traits that have led to some debate about their position in the primate taxonomy. They are widely considered members of the haplorrhine group because they share several key derived traits with monkeys, apes, and humans, including dry noses, a fovea, not having a tapetum lucidum, and having eyes that are close together. Tarsiers also have some traits that are more like strepsirrhines and some that are unique. Tarsiers are the only haplorrhine that are specialized vertical clinger leapers, a form of locomotion only otherwise seen in some strepsirrhines. Tarsiers actually get their name because their ankle (tarsal) bones are elongated to provide a lever for vertical clinging and leaping. Tarsiiformes are also small, with most species weighing between 100 and 150 grams. Like strepsirrhines, tarsiers are nocturnal, but because they lack a tapetum lucidum, tarsiers compensate by having enormous eyes. In fact, each eye of a tarsier is larger than its brain. These large eyes allow enough light in for tarsiers to still be able to see well at night without the reflecting layer in their eyes. To protect their large eyes, tarsiers have a partially closed postorbital plate that is somewhat intermediate between the postorbital bar of strepsirrhines and the full postorbital closure of other haplorrhines (Figure 5.23). Tarsiers have different dental formulas on their upper and lower teeth. On the top, the dental formula is 2:1:3:3, but on the bottom it is 1:1:3:3. Other unusual traits of tarsiers include having two grooming claws on each foot and the ability to rotate their heads around 180 degrees, a trait useful in locating insect prey. The tarsier diet is considered **faunivorous** because it consists entirely of animal matter, making them the only primate not to eat any vegetation. They are also only one of two living haplorrhines to be solitary, the other being the orangutan. Most tarsiers are not sexually dimorphic, like strepsirrhines, although males of a few species are slightly larger than females.



Figure 2.1.3.11: Skull of a tarsier showing very large eye sockets and partially closed postorbital plates.

Two alternative classifications have emerged due to the unusual mix of traits that tarsiers have. Historically, tarsiers were grouped with lemurs, lorises, and galagos into a suborder called Prosimii. This classification was based on tarsiers, lemurs, lorises, and galagos all having grooming claws and similar lifestyles (e.g., small, nocturnal, more leaping locomotion, diet heavy in insects, more solitary). Monkeys, apes, and humans were then separated into a suborder called the Anthropoidea. These suborder groupings were based on grade rather than clade. Today, most people use Suborders Strepsirrhini and Haplorrhini, which are clade groupings based on the derived traits that tarsiers share with monkeys, apes, and humans (e.g., more postorbital closure, fovea, no tapetum lucidum, dry nose). The Strepsirrhini/Haplorrhini dichotomy is also supported by the genetic evidence that indicates tarsiers are more closely related to monkeys, apes, and humans (Jameson et al. 2011). Figure 5.24 summarizes the unusual mix of traits seen in tarsiers.

Table 5.3.3: Tarsiers at a glance: Tarsiers have a mix of traits that lead to debate about their classification. Some of their traits superficially resemble strepsirrhines, but they share many derived traits with haplorrhines. They also possess unique characteristics that are unlike any other primates.

Like Strepsirrhini	Unique	Like Haplorrhini
Very small		Almost full PO closure
Nocturnal	Two grooming claws	More convergent eyes
Highly insectivorous	2:1:3:3/1:1:3:3 dental formula	No tapetum lucidum
Solitary	Do not eat vegetation	No rhinarium
Vertical clinger-leapers	Can rotate their heads nearly 180 degrees	Genetic evidence
Little/no sexual dimorphism		Fovea

Infraorder Platyrrhini of Central and South America



Figure 2.1.3.12: Geographic distribution of the platyrrhines across Central and South America. New World monkeys are the only naturally occurring non-human primates in the Americas.

The platyrrhines, also commonly called New World monkeys, are the only non-human primates in Central and South America (Figure 5.25) and so, like the lemurs of Madagascar, have diversified into a variety of forms in the absence of competition. Infraorder Platyrrhini get their name from their distinctive nose shape. “Platy” means flat and “rhini” refers to noses and, indeed,

New World monkeys have noses that are flat and wide, with nostrils that are far apart, facing outward, and usually round in shape (Figure 5.26). This nose shape is very different from what we see in catarrhines, the group that includes Old World monkeys, apes, and humans.

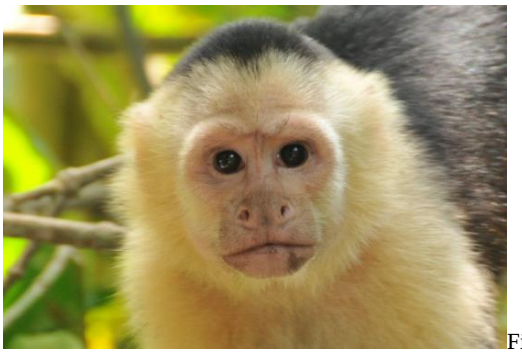


Figure 2.1.3.13: A capuchin monkey demonstrating a typical platyrrhine nose shape with round nostrils pointing outward on a flat nose.

On average, Platyrrhini are smaller and less sexually dimorphic than catarrhines, and they have retained the more primitive primate dental formula of 2:1:3:3. Platyrrhines are also all highly arboreal, whereas many Old World monkeys and apes spend significant time on the ground. The New World monkeys also differ in having less well-developed vision. This is reflected in the wiring in the visual system of the brain but also in their **polymorphic color vision**. The genes that enable individuals to distinguish reds and yellows from blues and greens are on the X chromosome. Different genes code for being able to see different wavelengths of light so to distinguish between them you need to be heterozygous for seeing color. In New World monkeys, each X chromosome carries the genes for seeing one wavelength. This means that male platyrrhines (having only one X chromosome) are always dichromatic. Female platyrrhines can be dichromatic (if they are homozygous for the same version of the color vision gene) or trichromatic (if they are heterozygous) (Kawamura et al. 2012). We currently know of two exceptions to this pattern among platyrrhines. Owl monkeys, which are nocturnal, are **monochromatic**, meaning that they cannot distinguish any colors. The other exception are Howler monkeys, which have evolved to have two color vision genes on each X chromosome. This means that both male and female howler monkeys are able to see reds and yellows. As we will discuss, all Old World monkeys, apes, and humans are trichromatic.

Platyrrhines include the smallest of the monkeys, the marmosets and tamarins (Figure 5.27). These small monkeys, all of which weigh less than 1 kilogram, live in cooperative family groups, wherein usually only one female reproduces and everyone else helps carry and raise the offspring. They are unusual primates in that they regularly produce twins. The diet of marmosets and tamarins largely consists of gums and saps, so these monkeys have evolved claw-like nails that enable them to cling to the sides of tree trunks like squirrels as well as special teeth that allow them to gnaw through bark. They also have one fewer molar than other platyrrhines, giving them a dental formula of 2:1:3:2.

The largest of the platyrrhines are a family that include spider monkeys, woolly spider monkeys, woolly monkeys, and howler monkeys (Figure 5.28). This group of monkeys can weigh up to 9–15 kg and have evolved prehensile tails that can hold their entire body weight. It is among this group that we see semi-brachiators, like the spider monkey (Figure 5.10). To make them more efficient in this form of locomotion, spider monkeys evolved to not have thumbs so that their hands work more like hooks that can easily let go of branches while swinging. Howler monkeys are another well-known member of this group, earning their name due to their loud calls, which can be heard for miles away. To make these loud vocalizations, howler monkeys have a specialized vocal system that includes a large larynx and hyoid bone. Howler monkeys are the most folivorous of the platyrrhines and are known for spending a large portion of their day digesting their food.

There are many other monkeys in the New World, including the gregarious capuchins (Figure 5.26) and squirrel monkeys, the pair-living titi monkeys, and the nocturnal owl monkeys. There are also the seed-eating monkeys such as saki monkeys and uakaris. In many areas across Central and South America, multiple different species of platyrrhine will share the forests, and some species will even travel together in associations that you will learn about in Chapter 6. According to molecular evidence, the diversity of platyrrhines that we see today seems to have originated about 25 million years ago (Schneider and Sampaio 2015). Figure 5.29 summarizes the key traits of platyrrhines relative to the other infraorders of Haplorrhini.



Figure 2.1.3.14: (Clockwise from top-right) golden-headed lion tamarin, pygmy marmoset, Goeldi's monkey, bare-eared marmoset, emperor tamarin, and common marmoset.



Figure 2.1.3.15: (Clockwise from top right) howler monkey, woolly monkey, woolly spider monkey, and spider monkey.

Platyrrhini traits
Flat nose with rounded nostrils pointing to the side
Highly arboreal
Less sexually dimorphic on average
2:1:3:3 dental formula*
Polymorphic color vision*

Platyrrhini at a glance: Summary of the key traits we use to distinguish platyrrhines. Traits indicated with an * are those with exceptions detailed in the text.

Infraorder Catarrhini of Asia and Africa

Infraorder Catarrhini includes Old World monkeys, apes, and humans. Non-human catarrhines are found all over Africa and South and Southeast Asia, with some being found as far north as Japan. The most northerly and southerly catarrhines are from the

superfamily that includes the Old World monkeys. In contrast, apes are less tolerant of drier, more seasonal environments and so have a relatively restricted geographic range.



Figure 2.1.3.16: A Wolf's guenon demonstrating a typical catarrhine nose with teardrop-shaped nostrils close together and pointed downward.

When compared to the other haplorrhine infraorders, catarrhines are distinguished by several characteristics. Catarrhines have a distinctive nose shape, with teardrop-shaped nostrils that are close together and point downward (Figure 5.30). Old World monkeys, apes, and humans also have one fewer premolar than most other primates, giving us a dental formula of 2:1:2:3 (Figure 5.31). On average, catarrhines are the largest and most sexually dimorphic group of primates. Gorillas are the largest of all living primates, with males weighing up to 220 kg. The most sexually dimorphic of all primates are mandrills. Mandrill males not only have much more vibrant coloration than mandrill females but also have larger canines and can weigh up to three times more (Setchell et al. 2001). The larger body size of catarrhines is related to the more terrestrial lifestyle of many members of this infraorder. In fact, the most terrestrial of living primates can be found in this group. Among all primate taxa, vision is the most developed in catarrhines. Catarrhines independently evolved the same adaptation as howler monkeys in having each X chromosome with sufficient genes to distinguish both reds and yellows, so all catarrhines are trichromatic. Trichromatic color vision is particularly useful to catarrhines, which are all diurnal.

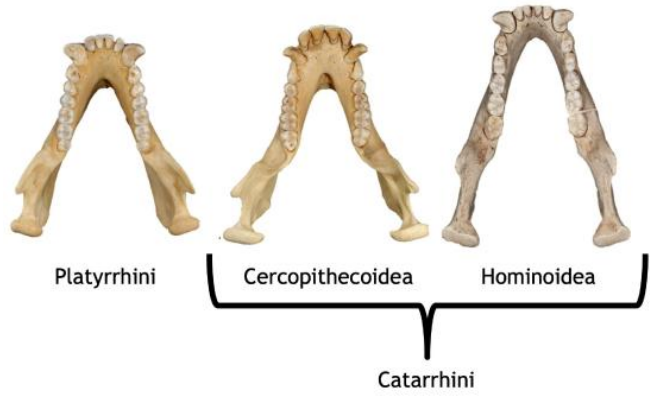


Figure 2.1.3.17: Catarrhines are distinguished in that they only have two premolars compared to the three premolars seen in most other primate taxa, including the platyrrhines shown here for comparison. In these images you can also see one of the derived traits of cercopithecoids, their bilophodont molars, which differ from the more primitive Y-5 molars that apes and humans have.

Infraorder Catarrhini is divided into two superfamilies: Superfamily Cercopithecoidea, which includes Old World monkeys, and Superfamily Hominoidea, which includes apes and humans. Molecular estimates place the split between cercopithecoids and hominoids at about 32 million years ago (Pozzi et al. 2014), which fits well with the fossil record showing evidence of the lineages by about 25 million years ago (see Chapter 8 on primate evolution).

Superfamily Cercopithecoidea of Africa and Asia

Compared to hominoids, Old World monkeys have a more primitive quadrupedal body plan (discussed later in Figure 5.39), but they do have a couple of derived traits shared by all members of this group. Cercopithecoidea have **bilophodont** molars ("bi" meaning two, "loph" referring to ridge, and "dont" meaning tooth). Referring back to Figure 5.31, you will see how the molars of cercopithecoids have four cusps arranged in a square pattern and have two ridges connecting them. It is thought that this molar enabled Old World monkeys to eat a wide range of foods, thus allowing them to live in habitats that apes cannot. The other key derived trait that all cercopithecoids share is having **ischial callosities** (Figure 5.32). The ischium is the part of your pelvis that you are sitting on right now (see Appendix A: Osteology). In Old World monkeys, this part of the pelvis has a flattened surface that, in living animals, will have callused skin over it. These function as seat pads for cercopithecoids, who often sit above branches when feeding and resting.

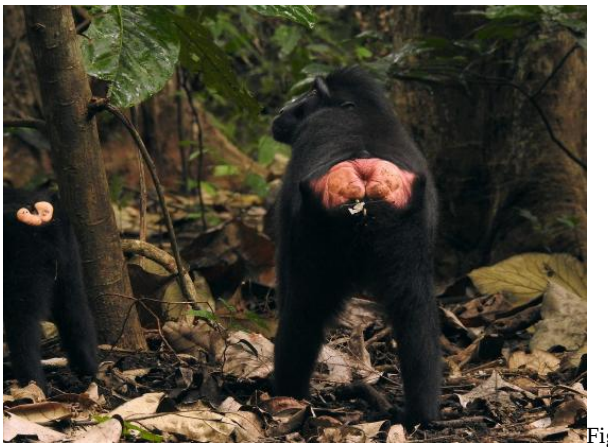


Figure 2.1.3.18: The second derived trait of cercopithecoids are their ischial callosities, shown here on a crested black macaque.

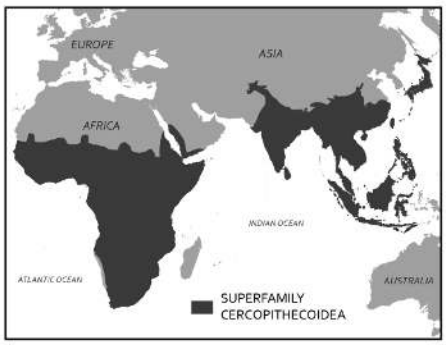


Figure 2.1.3.19: Geographic distribution of the Old World monkeys. Catarrhines have the widest geographic distribution due to the success of cercopithecoid monkeys who are found all across Africa and Asia.



Figure 2.1.3.20: Silver leaf monkey infants are born with orange fur, dramatically contrasting the adult coat color of their mothers. After a few months, the infants gradually change color to that of their parents.

The cercopithecoid monkeys are the most geographically widespread group of non-human primates (Figure 5.33). Since their divergence from hominoids, this monkey group has increased in numbers and diversity. In part, their success over hominoids is due to the faster reproductive rates of cercopithecoids relative to hominoids. On average, Old World monkeys will reproduce every one to two years, whereas hominoids will reproduce once every four to nine years, depending on the taxon.



Figure 2.1.3.21: Proboscis monkeys are one of several “odd-nosed” leaf monkeys. Male proboscis monkeys, like the one shown here, have large, pendulous noses. Female proboscis monkey noses are much smaller; in this species nose size is a sexually dimorphic trait.

Cercopithecoidea is split into two groups, the leaf monkeys and the cheek-pouch monkeys. Both groups coexist in Asia and Africa; however, the majority of leaf monkey species live in Asia with only a few taxa in Africa. In contrast, only one genus of cheek-pouch monkey lives in Asia, and all the rest of them in Africa. As you can probably guess based on their names, the two groups differ in terms of diet. Leaf monkeys are primarily folivores, with some species eating a significant amount of seeds. Cheek-pouch monkeys tend to be more frugivorous or omnivorous, with one taxon, geladas, eating primarily grasses. The two groups also differ in some other interesting ways. Leaf monkeys tend to produce infants with **natal coats**—infants whose fur is a completely different color from their parents (Figure 5.34). Leaf monkeys are also known for having odd noses (Figure 5.35), and so they are sometimes called “odd-nosed monkeys.” Cheek-pouch monkeys are able to pack food into their cheek pouches (Figure 5.36), thus allowing them to move to a location safe from predators or aggressive individuals of their own species where they can eat in peace.



Figure 2.1.3.22: This bonnet macaque has filled its cheek pouches with food. This adaptation is useful in transporting food to a safer location to eat.



Figure 2.1.3.23: Because of important monkey-like figures in the Hindu religion, macaques are protected in India and often live near temples where they are fed by local peoples.

In the introduction to this chapter, I mentioned the innate affinity that humans have toward non-human primates even when we do not fully understand our exact relationship to them. In fact, recognition of similarities between humans and other primates is very ancient, dating back far earlier than Linnaeus. For many of us, we only ever get to see primates in zoos and animal parks, but in many areas of the world, humans have coexisted with these animals for thousands of years. In areas where humans and primates have a long, shared history, non-human primates often play key roles in creation myths and cultural symbolism.

Hamadryas baboons feature significantly in Ancient Egyptian iconography. Ancient Egyptian deities and beliefs transformed over time, as did the role of hamadryas baboons. Early on, baboons were thought to represent dead ancestors, and one monkey deity, called Babi or Baba, was thought to feed off of dead souls. Later, baboons became the totem animal for Thoth, the deity of science, writing, wisdom, and measurement, who also wrote the book of the dead. Sunbathing hamadryas baboons led ancient Egyptians to associate them with Ra, the sun god, who was the son of Thoth. During mummification, human organs were removed and put into canopic jars, one of which was topped with the head of the baboon-headed god, Hapi. Hamadryas baboons were also often kept as pets, as depicted in hieroglyphics, and occasionally mummified as well.

On Madagascar, indris and aye-ayes play roles in the creation myths and omens of local people. There are many myths regarding the origins of indris and their relationship to humans, including one where two brothers living in the forest separated, with one brother leaving the forest and becoming a human while the other stayed in the forest to become the indri. Indris are considered sacred and are therefore protected, due to their similarities to humans in having long legs, no tail, and upright posture. Unfortunately, the aye-aye is not treated with the same reverence. Aye-ayes, due to their unusual appearance, are thought to be omens of death. They are usually killed when encountered because it is believed that someone will die if an aye-aye points at them.

In India, monkeys play a key role in the Hindu religion. Hanuman, who resembles a monkey, is a key figure in the Ramayana. Hanuman is thought to be a guardian deity, and so local monkeys like Hanuman langurs and macaques are protected in India (Figure 5.37). In Thailand, where Hinduism is also practiced, the Hindu reverence for monkeys extends to “monkey feasts,” where large quantities of food are spread out in gratitude to the monkeys for bringing good fortune.

The people of Japan have coexisted with Japanese macaques for thousands of years, and so monkeys play key roles in both of the major Japanese religions. In the Shinto religion, macaques are thought of as messengers between the spirit world and humans and monkey symbols are thought to be good luck. The other major religion in Japan is Buddhism, and monkeys play a role in symbolism of this religion as well. The “Three Wise Monkeys” who see no evil, speak no evil, and hear no evil derive from Buddhist iconography of monkeys.

In the New World, monkeys feature often in Mayan and Aztec stories. In the Mayan creation story, the Popol Vuh, the “hero brothers” are actually a howler monkey and a spider monkey, who represent ancestors of humans in the story. In the Aztec religion, spider monkeys are associated with the god of arts, pleasure, and playfulness. A spider monkey is also represented in a Peruvian Nazca geoglyph, a large design made on the ground by moving rocks.

In many of these regions today, the relationships between humans and non-human primates are complicated. The bushmeat and pet trades make these animals valuable at the expense of many animals’ lives, and in some areas, non-human primates have become pests who raid crop fields and consume valuable foods. All of this has led to the development of a new subarea of anthropology

called **Ethnoprimatology**, which involves studying the political, economic, symbolic, and practical relationships between humans and non-human primates. This field highlights the particular challenges for humans of having to coexist with animals with whom we share so much in common. It also provides insight into some of the challenges facing primate conservation efforts (see Appendix A: Primate Conservation).

Superfamily Hominoidea of Africa and Asia

Figure 2.1.3.23: Geographic distribution of apes across Central and West Africa, and Southeast Asia. Hominoids overlap geographically with cercopithecoid monkeys but have a lower tolerance for seasonal environments and so are found only in tropical forests across these regions.

The Superfamily Hominoidea of Africa and Asia (Figure 5.38) includes the largest of the living primates, apes and humans, but our superfamily differs from other primates in some other key ways as well. When compared to cercopithecoids, hominoids have more primitive teeth. Whereas Old World monkeys have bilophodont molars, hominoids have Y-5 molars, which feature five cusps separated by a "Y"-shaped groove pattern (Figure 5.31). The Y-5 molar was present in the common ancestors of hominoids and cercopithecoids, thus telling us it is the more primitive molar pattern of the two. Where hominoids differ the most from other primates, however, is in our body plans. This is due to the unusual form of locomotion that hominoids are adapted for, brachiation (Figure 5.39).

	Quadrupedalism	**Brachiation**
Arm length vs. leg length	About equal	Arms are longer
Shoulder position	More on the front	Out to the side
Ribcage shape	Deep front-to-back Narrow side-to-side	Shallow front-to-back Wide side-to-side
Length of lower back	Long	Short
Collar bone length	Short	Long
Ulnar olecranon process	Long	Short
Ulnar styloid process	Long	Short
Tail	Short to long	None

Figure 5.39 Quadrupedalism vs. brachiation: Summary of the key anatomical differences between a quadrupedal primate and one adapted for brachiation. To view and compare these traits using photos of bones, check out the interactive skeletal websites listed under the "Further Explorations" section at the end of this chapter.

To successfully swing below branches, many changes to the body needed to occur. The arms of a hominoid are much longer than the legs in order to increase reach, and the lower back is shorter and less flexible to increase control when swinging. The torso, shoulders, and arms of hominoids have evolved to increase range of motion and flexibility (Figure 5.9). The clavicle, or collar bone, is longer in order to stabilize the shoulder joint out to the side, thus enabling us to rotate our arms 360 degrees.Our rib cages are wider side to side and shallower front to back than those of cercopithecoids and we do not have tails, as tails are useful for balance when running on all fours but not useful when swinging. Hominoids also have modified ulnae, one of the two bones in the forearm (see Appendix A: Osteology). At the elbow end of the ulna, hominoids have a short **olecranon process**, which allows for improved extension in our arms. At the wrist end of the ulna, hominoids have a short **styloid process**, which enables us to have very flexible wrists, a trait critical for swinging. Both the olecranon process and styloid process are long in quadrupedal animals who carry much of their weight on their forelimbs when traveling and who therefore need greater stability rather than flexibility in those joints.

Apes and humans also differ from other primates in behavior and life history characteristics. Hominoids all seem to show varying degrees of female dispersal at sexual maturity. Dispersal refers to leaving the area or group where an individual was born. As you will learn about in Chapter 6, it is more common that males leave. Indeed, some apes show males dispersing in addition to females, but the broader tendency for female dispersal in hominoids is a bit unusual among primates. Our superfamily is also characterized by the most extended life histories of all primates. All members of this group live a long time and take a long time to grow and start reproducing. Hominoids also reproduce much less frequently compared to cercopithecoid monkeys. The slow pace of this life

history is likely related to why hominoids have decreased in diversity since they first evolved. In the past, hominoids were tremendously diverse in both geography and adaptations. Today, there are only five types of hominoids left: gibbons and siamangs, orangutans, gorillas, chimpanzees and bonobos, and humans.

Infraorder Catarrhini	
Downward facing, tear-drop shaped nostrils, close together Arboreal and more terrestrial taxa On average, largest primates On average, most sexually dimorphic taxonomic group 2:1:2:3 dental formula All trichromatic	
 **Superfamily Cercopithecoidea**	 **Superfamily Hominoidea**
Wide geographic distribution Bilophodont molars Ischial callosities Reproduce every 1-2 years	Tropical forests of Africa and Asia Y-5 molars Adaptations for brachiation Reproduce every 4-9 years

Figure 5.40 Catarrhini at a glance: Summary of key traits of the Infraorder Catarrhini as well as the characteristics used to distinguish between the two superfamilies within this group.

Family *Hylobatidae* of Southeast Asia



Figure 2.1.3.24: Siamangs are the largest of the Hylobatidae family. They are all black and, as you can see inflated in this photo, have a throat sac that they use to give loud calls.

The number of genera in this group has been changing in recent years, but the taxa included can broadly be discussed as gibbons and siamangs. Both are found across Southeast Asian tropical forests. These are the smallest of the hominoids and so are sometimes referred to as the “lesser apes.” Gibbons weigh, on average, about 13 pounds and tend to be more frugivorous, whereas siamangs are about twice the size of gibbons and are more folivorous. Unlike the larger-bodied apes (orangutans, chimps, bonobos, and gorillas) who make nests to sleep in every night, gibbons and siamangs will develop callused patches on their ischium resembling ischial callosities. There are many different gibbon species that vary in their coloration and markings. Siamangs, however, are all black with big throat sacs that are used in their exuberant vocalizations (Figure 5.41). Both gibbons and siamangs live in pairs with very little sexual dimorphism, although males and females do differ in coloration in some species.

Pongo of Southeast Asia



Figure 2.1.3.25: A female orangutan and her infant.



Figure 2.1.3.26: A flanged adult male. Male orangutans are about twice the size of females, and in these photos you can also see the sexual dimorphism in coat length, cheek flanges and throat sac in the male.

The Genus *Pongo* refers to orangutans. These large red apes are found on the islands of Borneo and Sumatra in Southeast Asia. There are two well-known species of orangutan, one on each island. Recently, a third, very rare species was discovered in Southern Sumatra (Nater et al. 2017). Orangutans are highly frugivorous but will supplement their diet with leaves and even bark when fruit is less available. As mentioned earlier, orangutans are the only diurnal, solitary taxon among primates and are extremely slow to reproduce, producing only one offspring about every seven to nine years. They are highly sexually dimorphic (Figure 5.42), with fully developed, “flanged” males being approximately twice the size of females. These males have large throat sacs; long, shaggy coats; and cheek flanges.The skulls of male orangutans often feature a **sagittal crest**, which is believed to function as both additional attachment area for chewing muscles but also in sexual competition (Balolia et al. 2017). An unusual feature of orangutan biology is **male bimaturism**. Male orangutans are known to delay maturation until one of the more dominant, flanged males disappears. The males that delay maturation are called “unflanged” males, and they can remain in this state for their entire life. Unflanged males resemble females in their size and appearance and will sneak copulations with females while avoiding the bigger, flanged males. Flanged and unflanged male orangutans represent alternative reproductive strategies, both of which successfully produce offspring (Utami et al. 2002).

Gorilla of Africa



Figure 2.1.3.27: A female gorilla and her offspring.



Figure 2.1.3.28: A silverback male. Male gorillas are about twice the size of females, but also differ from females in having a large sagittal crest, and silver back, which appears as they mature.

There are several species of gorillas that can be found across Central Africa. Gorilla males, like orangutan males, are about twice the size of female gorillas (Figure 5.43). When on the ground, gorillas use a form of quadrupedalism called knuckle-walking, where the fingers are curled under and the weight is carried on the knuckles. Male gorillas have a large sagittal crest and larger canines compared with females. Adult male gorillas are often called “silverbacks” because when they reach about twelve to thirteen years old, the hair on their backs turns silvery gray. Gorillas typically live in groups of one male and several females. Gorillas are considered folivorous, although they can be more frugivorous depending on fruit seasonality (Remis 1997).

Pan of Africa



Figure 2.1.3.29: Bonobo, Pan paniscus. You can see the distinctive hair-part on this bonobo.

The Genus *Pan* includes two species: *Pan troglodytes* (the common chimpanzee) and *Pan paniscus* (the bonobo). These species are separated by the Congo River, with chimpanzees ranging across West and Central Africa and bonobos located in a restricted area south of the Congo River. Chimpanzees and bonobos both have broad, largely frugivorous diets and similar social groups. The two species differ morphologically in that bonobos are slightly smaller, have their hair parted down the middle of their foreheads, and are born with dark faces (Figure 5.44). In contrast, chimpanzees do not have the distinctive parted hair and are born with light faces which darken as they mature (Figure 5.45). Chimpanzees and bonobos live in a grouping called a fission-fusion community, which you will learn more about in Chapter 6. Both species are moderately sexually dimorphic, with males about 20% larger than females. When on the ground, chimpanzees and bonobos knuckle-walk like gorillas do.



Figure 2.1.3.30: A common chimpanzee, Pan troglodytes, female and her offspring. Note the pink face of the youngest individual. Bonobos are born with dark-skinned faces, but chimpanzees are born with pink faces that darken with age.

Homo

The last member of the Hominoidea to discuss is our own taxon, *Genus Homo*. Humans differ from apes in many aspects of our morphology, behavior, and life history, all of which you will be learning about in later chapters. One of the objectives of this chapter, however, and of biological anthropology in general, is to understand our place in nature. This means looking for the aspects of human biology that lead us to place humans within the taxonomic diversity we have just discussed. To accomplish this, we not only consider how humans are different from other species but also examine the traits that unite us with the other primates, our similarities—that is our focus here.

There are clear similarities between humans and the other apes in our morphology and life history. Like other hominoids, humans lack a tail and possess upper-body adaptations for brachiation. While our lower body has been modified for a bipedal gait, we are still able to swing from branches or "monkey bars," or throw a fastball, all thanks to our mobile shoulder joint. Humans, like other hominoids, also have a Y-5 cusp pattern on our molars. As discussed earlier, all hominoids have an extended life history, taking a long time to grow and develop, and have a long life span. Humans, too, exhibit these same characteristics. Lastly, while humans show a great deal of variation across cultures, many human societies show patterns of female dispersal in which males stay in the group into which they were born while females leave (Burton et al. 1996).

Among the hominoids, humans show particular affinities with other members of the African Clade, *Pan* and *Gorilla*. Humans share over 96% of our DNA with gorillas (Scally et al. 2012), and over 98% with *Pan* (Ebersberger et al. 2002). Even without this strong genetic evidence, the African Clade of hominoids share many morphological similarities. These shared traits include eye sockets that are slightly farther apart and are more square or rounded compared to the closely placed, ovoid eyes of orangutans. Also, the cheekbones of the African clade sweep backward compared to the more flattened orangutan cheekbones. Today, *Pan* and *Gorilla* knuckle-walk when on the ground, and it has been suggested that the last common ancestor of chimpanzees, bonobos, gorillas, and humans shared this trait (Richmond et al. 2001).

Our closest living relatives today are chimpanzees and bonobos. Because of our close relationship, humans share many additional traits in common with *Pan*. Humans, chimpanzees, and bonobos all live in similar social groups that are characterized by territoriality and male cooperation, among other things. Chimpanzee males are well-known to cooperate in hunting, a common trait across human societies as well. As you will learn more about in the next chapter, chimpanzee populations have also been observed to make and use tools for different purposes, not unlike what humans do.

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2.1.4: Learning From Primates

While primates are fascinating animals in their own right, we study non-human primates in anthropology with the ultimate goal of understanding more about our own biology and evolutionary history. The close relationship between humans and non-human primates makes them excellent for studying humans via **homology,** looking at traits that are shared between two taxa because they inherited the trait from a common ancestor. Consider, for example, the characteristics discussed in the previous section that are shared by humans and *Pan*. Since both taxa exhibit these traits, they are likely *homologous*, meaning these shared traits were probably present in the last common ancestor of humans and *Pan* approximately 6-8 million years ago .

Non-human primates also make excellent comparators for learning about humans via **analogy** (sometimes called convergent evolution, parallel evolution, or homoplasy). Many non-human primates live in environments or social groups similar to those in which our ancestors lived and therefore exhibit similar behavioral and morphological traits as what we see in humans. For example, baboons and humans share the trait of having long legs. In humans, this is because about 1.7 million years ago, our ancestors moved into open savanna habitats, like those baboons live in today, and longer legs enabled them to move over long distances more efficiently. Baboons independently evolved longer arms and legs for the same reason—to be able to cover more ground, more efficiently, in an open habitat. This means that having long legs is an *analogous* trait in baboons and humans—that is, this adaptation evolved independently in the two species but for the same purpose.

Conclusion

The Order Primates is a diverse and fascinating group of animals united in sharing a suite of characteristics—visual specialization, grasping hands and feet, large brains, and extended life histories—that differentiates us from other groups of mammals. In this chapter, we surveyed the major taxonomic groups of primates, discussing where humans fit among our close relatives as well as discovering that primates are interesting animals in their own right. We discussed a range of key traits used to distinguish between the many taxa of living primates, including dietary, locomotor, and behavioral characteristics. Because of our long, shared evolutionary history with these animals, non-human primates provide a crucial resource for understanding our current biology.In the next chapter, you will discover the fascinating and complex social behaviors of non-human primates which provide further insight into our evolutionary biology.

Review Questions

- Why does the field of anthropology, a field dedicated to the study of humans, include the study of non-human animals? What important things can we learn from non-human primates in anthropology?
- One of the important goals of an introductory biological anthropology course is to teach you about your place in nature. What is the full taxonomic classification of humans, and what are some of the traits we have of each of these categories?
- When you have seen primates in person, did you observe any facial expressions, behaviors, or physical traits that seemed familiar to you? If so, which ones and why?
- Why is it important to try to place taxa into a clade classification rather than groupings based on grade? Can you think of an example?
- Draw out a tree showing the major taxonomic group of primates described here, making sure to leave room in between each level. Underneath each taxon, list some of the key features of this group so that you can compare traits between groups.

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2.1.5: Key Terms

Activity pattern: Refers to the time of day an animal is typically active.

African clade: A grouping that includes gorillas, chimpanzees, bonobos, humans, and their extinct relatives.

Analogy: When two or more taxa exhibit similar traits that have evolved independently, the similar traits evolve due to similar selective pressures. (Also sometimes called convergent evolution, parallel evolution, or homoplasy.)

Arboreal: A descriptor for an organism that spends most of its time in trees.

Asian clade: A grouping that includes orangutans and their extinct relatives.

Bilophodont: Molar pattern of cercopithecoid monkeys in which there are usually four cusps that are arranged in a square pattern and connected by two ridges.

Bipedalism: Walking on two legs.

Brachiation: A form of locomotion in which the organism swings below branches using the forelimbs.

Bunodont: Low, rounded cusps on the cheek teeth.

Canines: In most primates, these are the longest of the teeth, often conical in shape and used as a weapon against predators or others of their species.

Cathemeral: Active throughout the 24-hour period.

Clade: A grouping based on ancestral relationships; a branch of the evolutionary tree.

Cusps: The bumps on the chewing surface of the premolars and molars, which can be quite sharp in some species.

Dental formula: The number of each type of tooth in one quadrant of the mouth, written as number of incisors: canines: premolars: molars.

Derived trait: A trait that has been recently modified, most helpful when assigning taxonomic classification.

Diastema: A space between the teeth, usually for large canines to fit when the mouth is closed.

Dichromatic: Being able to see only blues and greens.

Diurnal: Active during the day.

Dry nose: The nose and upper lip are separated and the upper lip can move independently; sometimes referred to as a “hairy” or “mobile” upper lip.

Ethnoprimatology: A subarea of anthropology that studies the complexities of human-primate relationships in the modern environment.

Evolutionary trade-off: When an organism, which is limited in the time and energy it can put into aspects of its biology and behavior, is shaped by natural selection to invest in one adaptation at the expense of another.

Faunivorous: Having a diet consisting of animal matter: insects, eggs, lizards, etc.

Frugivore: Having a diet consisting primarily of fruit.

Folivore: Having a diet consisting primarily of leaves.

Fovea: A depressed area in the retina at the back of the eye containing a concentration of cells that allow us to focus on objects very close to our face.

Generalized trait: A trait that is useful for a wide range of tasks.

Grade: A grouping based on overall similarity in lifestyle, appearance, and behavior.

Grooming claw: A claw present on the second pedal digit in strepsirrhines.

Gummivore: Having a diet consisting primarily of gums and saps.

Heterodont: Having different types of teeth.

Homodont: Having only one type of tooth.

Homology: When two or more taxa share characteristics because they inherited them from a common ancestor.

Hone: When primates sharpen their canines by wearing them on adjacent teeth.

Incisors: The spatula-shaped teeth at the front of the mouth.

Insectivore: Having a diet consisting primarily of insects.

Ischial callosities: A flattened area of the ischium on the pelvis over which calluses form; functioning as seat pads for sitting and resting atop branches.

Knuckle-walking: A form of quadrupedal movement used by *Gorilla* and *Pan* when on the ground, where the front limbs are supported on the knuckles of the hands.

Life history: Refers to an organism's pace of growth, reproduction, lifespan, etc.

Locomotion: How an organism moves around.

Male bimaturism: Refers to the alternative reproductive strategies in orangutans in which males can delay maturation, sometimes indefinitely, until a fully mature, "flanged" male disappears.

Molars: The largest teeth at the back of the mouth; used for chewing; in primates, these teeth usually have between three and five cusps.

Monochromatic: Being able to see only in shades of light to dark, no color.

Monomorphic: When males and females of a species do not exhibit significant sexual dimorphism.

Natal coat: Refers to the contrasting fur color of baby leaf monkeys compared to adults.

Nocturnal: Active at night.

Olecranon process: Bony projection at the elbow end of the ulna.

Opposable thumb or **opposable big toe:** Having thumbs and toes that go in a different direction from the rest of the fingers, allows for grasping with hands and feet.

Pentadactyly: Having five digits or fingers and toes.

Polymorphic color vision: A system in which individuals of a species vary in their abilities to see color. In primates, it refers to males being dichromatic and females being either trichromatic or dichromatic.

Postorbital bar: A bony ring that surrounds the eye socket, open at the back.

Postorbital closure/plate: A bony plate that provides protection to the side and back of the eye.

Prehensile tail: A tail that is able to hold the full body weight of an organism, which often has a tactile pad on the underside of the tip for improved grip.

Premolars: Smaller than the molars, used for chewing. In primates, these teeth usually have one or two cusps.

Primitive trait: A trait that has been inherited from a distant ancestor.

Quadrupedalism: Moving around on all fours.

Rhinariums: Wet noses; produced when the nose is connected to the upper lip.

Sagittal crest: A bony ridge along the top/middle of the skull, used for attachment of chewing muscles.

Scent marking: The behavior of rubbing scent glands or urine onto objects as a way of communicating with others.

Semi-brachiation: A form of locomotion in which an organism swings below branches using a combination of forelimbs and prehensile tail.

Sexually dimorphic: When a species exhibits sex differences in morphology, behavior, hormones, and/or coloration.

Shearing crests: Sharpened ridges that connect cusps on a bilophodont molar.

Specialized trait: A trait that has been modified for a specific purpose.

Styloid process of ulna: A bony projection of the ulna at the end near the wrist.

Tactile pads: Sensitive skin at the fingertips for sense of touch. Animals with a prehensile tail have a tactile pad on the underside of the tail as well.

Tapetum lucidum: Reflecting layer at the back of the eye that magnifies light.

Terrestrial: Spending most of the time on the ground.

Tetrachromatic: Having the ability to see reds, yellows, blues, greens, and ultraviolet.

Tooth comb or **dental comb:** A trait of the front, lower teeth of strepsirrhines in which, typically, the four incisors and canines are long and thin and protrude outward.

Trichromatic color vision: Being able to distinguish yellows and reds in addition to blues and greens.

Vertical clinging and leaping: A locomotor pattern in which animals are oriented upright while clinging to vertical branches, push off with hind legs, and land oriented upright on another vertical branch.

Y-5 molar: Molar cusp pattern in which five molar cusps are separated by a “Y”-shaped groove pattern.

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SECTION OVERVIEW

2.2: Primate Evolution

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Learning Objectives

- Understand the major trends in primate evolution from the origin of primates to the origin of our own species.
- Learn about primate adaptations and how they characterize major primate groups.
- Discuss the kinds of evidence that anthropologists use to find out how extinct primates are related to each other and to living primates.
- Recognize how the changing geography and climate of Earth have influenced where and when primates have thrived or gone extinct.

The first fifty million years of primate evolution was a series of adaptive radiations leading to the diversification of the earliest lemurs, monkeys, and apes. The primate story begins in the canopy and understory of conifer-dominated forests, with our small, furtive ancestors subsisting at night, beneath the notice of day-active dinosaurs.

From the archaic **plesiadapiforms** (archaic primates) to the earliest groups of true primates (**euprimates**), the origin of our own order is characterized by the struggle for new food sources and microhabitats in the arboreal setting. Climate change forced major extinctions as the northern continents became increasingly dry, cold, and seasonal and as tropical rainforests gave way to deciduous forests, woodlands, and eventually grasslands. Lemurs, lorises, and tarsiers—once diverse groups containing many species—became rare, except for lemurs in Madagascar where there were no anthropoid competitors and perhaps few predators. Meanwhile, **anthropoids** (monkeys and apes) emerged in the **Old World**, then dispersed across parts of the northern hemisphere, Africa, and ultimately South America. Meanwhile, the movement of continents, shifting sea levels, and changing patterns of rainfall and vegetation contributed to the developing landscape of primate biogeography, morphology, and behavior. Today's primates provide modest reminders of the past diversity and remarkable adaptations of their extinct relatives. This chapter explores the major trends in primate evolution from the origin of the Order Primates to the beginnings of our own lineage, providing a window into these stories from our ancient past.

2.2.1: How to Diagnose a Primate

2.2.2: Major Hypotheses About Primate Origins

2.2.3: The Origin of Primates

2.2.4: The Emergence of Modern Primate Groups

2.2.5: Planet of Apes

2.2.6: Key Terms

Review Questions

- Compare three major hypotheses about primate origins, making reference to each one's key ecological reason for primate uniqueness.
- Explain how changes in temperature, rainfall, and vegetation led to major changes in primate biogeography over the Early Tertiary.
- List some euprimate features that plesiadapiforms have and some that they lack.
- Contrast adapoids and omomyoids in terms of life habits.
- Describe one piece of evidence for each of the adapoid, omomyoid, and tarsier origin hypotheses for anthropoids.

- Discuss the biogeography of the origins of African great apes and orangutans using examples from the Miocene ape fossil record.

About the Authors

Jonathan Perry



Jonathan Perry

Jonathan Perry was trained as a paleontologist and primatologist at the University of Alberta, Duke University, and Stony Brook University. His research focuses on the relationship between food, feeding, and craniodental anatomy in primates both living and extinct. This work includes primate feeding behavior, comparative anatomy, biomechanics, and field paleontology. For the past six years, he has taught courses on primate evolution at the undergraduate and graduate level.

Stephanie Canington



Stephanie Canington

Stephanie Canington is a Ph.D. student. Her current research is on the links between food properties, feeding behavior, and jaw morphology in lemurs that live in varying forms of captivity.

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Tables

Table 8.1. Major Families of Fossil Primates Discussed Here

Broad Group	Family	Example Taxon	Approximate Age for Group [1]
Plesiadapiforms	Paromomyidae	*Ignacius*	Middle Paleocene–Late Eocene
	Carpolestidae	*Carpolestes*	Late Paleocene–Early Eocene
	Plesiadapidae	*Plesiadapis*	Late Paleocene–Early Eocene
Early Euprimates	Asiadapidae	*Asiadapis*	Early Eocene
	Cercamoniidae	*Donrussellia*	Early Eocene
	Omomyidae	*Teilhardina*	Early Eocene
	Caenopithecidae	*Darwinius*	Eocene
	Adapidae	*Notharctus*	Middle Eocene
	Sivaladapidae	*Sivaladapis*	Late Miocene
Early Anthropoids	Eosimiidae	*Eosimias*	Middle Eocene
	Amphipithecidae	*Amphipithecus*	Middle–Late Eocene
	Oligopithecidae	*Catopithecus*	Late Eocene
	Proteopithecidae	*Proteopithecus*	Late Eocene
	Parapithecidae	*Apidium*	Early Oligocene
	Propliopithecidae	*Aegyptopithecus*	Early Oligocene
	Homunculidae	*Homunculus*	Early–Middle Miocene
Later Anthropoids	Proconsulidae	*Proconsul*	Early Miocene
	Victoriapithecidae	*Victoriapithecus*	Middle Miocene
	Pliopithecidae	*Pliopithecus*	Middle–Late Miocene
	Hylobatidae	*Yuanmoupithecus*	Late Miocene
	Hominidae	*Gigantopithecus*	Late Miocene–Pleistocene

[1] Derived from Fleagle (2013).

Table 8.2. Morphological Comparisons Between Early Euprimates and Extant Primates

Group	Similarities to Strepsirrhines	Similarities to Haplorhines
Adapoids	- Ring-shaped tympanic bone - Similar wrist and ankle bones - Similar molars	- Fusion of mandibular symphysis (in some adapoids and in all anthropoids but not in tarsiers) - Similarly small incisors - Sexual dimorphism in some taxa
Omomyoids	- Small and nocturnal - Unfused mandibular symphysis - Postorbital bar	- Large eyes - Tube-like tympanic bone (in some omomyoids and in catarrhines and tarsiers) - Pointy incisors - General skull proportions - Proportions of some ankle bones - "Leaping" femur (tarsiers)

Figure Attributions

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Figure 8.7 Representative crania of adapids (European adapoids) from the Museum d'Histoire Naturelle Victor Brun in Montauban, France original to Explorations: An Open Invitation to Biological Anthropology by Jonathan M. G. Perry is under a CC BY-NC 4.0 License.

Figure 8.8 Darwinius masillae holotype slabs by Jens L. Franzen, Philip D. Gingerich, Jörg Habersetzer1, Jørn H. Hurum, Wighart von Koenigswald, B. Holly Smith. Originally from Franzen et al. 2009. Complete Primate Skeleton from the Middle Eocene of Messel in Germany: Morphology and Paleobiology. *PLoS ONE* 4(5): e5723. doi.org/10.1371/journal.pone.0005723. Used under a CC BY 2.5 License.

Figure 8.9 Paleogeographic map showing hypothetical migration routes of *Teilhardina* by Smith et. al. Originally from Smith, Thierry, Kenneth D. Rose, and Philip D. Gingerich. 2006. Rapid Asia–Europe–North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene–Eocene Thermal Maximum. Proceedings of the National Academy of Sciences 103 (30): 11,223-11,227. doi:10.1073/pnas.0511296103.

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Figure 8.12 Egyptian workers sweeping Quarry I in the Fayum Basin (2004) by Jonathan M. G. Perry is under a CC BY-NC 4.0 License.

Figure 8.13 Elwyn Laverne Simons excavating Aegyptopithecus in the Fayum Basin used by permission of the Duke Lemur Center, Division of Fossil Primates.

Figure 8.14 Female and male cranium of *A. zeuxis* by Simons, Elwyn L., Erik R. Seiffert, Timothy M. Ryan, and Yousry Attia. Original from Simons, et al. 2007. A remarkable female cranium of the early Oligocene anthropoid *Aegyptopithecus zeuxis* (Catarrhini, Propliopithecidae). *Proceedings of the National Academy of Sciences of the United States of America* 104 (21): 8,731-8,736. doi.org/10.1073/pnas.0703129104.

Figure 8.15 Cast of the right half of the mandible of *Eosimias centennicus*, type specimen, from K.D. Rose cast collection, photo by Jonathan M. G. Perry is under a CC BY-NC 4.0 License.

Figure 8.16 Casts of representative amphipithecid material from K.D. Rose cast collection, photo by Jonathan M. G. Perry is under a CC BY-NC 4.0 License.

Figure 8.17 Representative specimens of *Homunculus patagonicus* from K.D. Rose cast collection, photo by Jonathan M. G. Perry is under a CC BY-NC 4.0 License.

Figure 8.18a Cañadon Palos Field Locality in Argentina by Jonathan M. G. Perry is under a CC BY-NC 4.0 License.

Figure 8.18b Swift Current Creek locality, Saskatchewan, Canada by Jonathan M. G. Perry is under a CC BY-NC 4.0 License.

Figure 8.19 Miocene Map with Fossil Ape Localities original to Explorations: An Open Invitation to Biological Anthropology by Elyssa Ebding at GeoPlace, California State University, Chico is under a CC BY-NC 4.0 License. Localities based on p. 311 of Fleagle, John G. 2013. Primate Adaptation and Evolution, Third Edition. San Diego, CA: Academic Press.

Figure 8.20 Range chart for Miocene hominoids of Western Eurasia by Casanovas-Vilar, Isaac, David M. Alba, Miguel Garcés, Josep M. Robles, and Salvador Moyà-Solà. Original from Casanovas-Vilar et al. 2011. Updated chronology for the Miocene hominoid radiation in Western Eurasia. *Proceedings of the National Academy of Sciences* 108 (14): 5,554-5,559.

Figure 8.21 Victoriapithecus macinnesi skull photo taken at the Musee d'Histoire Naturelle, Paris by Ghedoghedo is used under a CC BY-SA 3.0 License.

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2.2.1: How to Diagnose a Primate

When you examine the skeleton of a mammal, how do you know if you are looking at a primate? Some physical traits are useful in the **diagnosis** of primates and have been used to make decisions about which living and fossil mammals belong in our definition of the Order Primates. However, primates are hard to diagnose. There is no obvious diagnostic trait of our own order. From the first modern attempts to classify primates, scientists have struggled to come up with traits that are possessed exclusively and universally by primates. In the end, most have generated lists of traits that are of variable utility in making a correct diagnosis.

In the 19th century, British naturalist St. George Jackson Mivart articulated the most famous diagnosis of the Order Primates. This "primate pattern" is a list of the following traits: nails, clavicles, placentation, orbits encircled by bone, three tooth types (i.e., incisors, canines, premolars/molars), posterior lobe of the brain, calcarine fissure of the brain, opposable thumb and/or big toe, nail on the big toe, well-developed cecum, pendulous penis, testes within a scrotum, and two nipples in the pectoral region. Many primatologists have pointed out that no single feature on this list is unique to primates. Also, nails appear twice. Taken together, perhaps it is a useful list. Unfortunately, some of these traits (e.g., three types of teeth) are neither clear nor true of all primates. Other traits, like nipple number and location, are quite variable among primates. Still others, for example the pendulousness of the penis, can be assessed in only males.

Modifications of this approach by subsequent scientists have included lists of trends, like that suggested by Le Gros Clark. Clark's trends emphasize the flexibility and generalized nature of the limbs, mobility and dexterity of the digits, reduction of the snout with elaboration of the visual system, retention of simple teeth, and elaboration of the brain with prolonged period of juvenile dependence. Later, Robert D. Martin emphasized distinctive reproductive characteristics of primates, along with details of cranial anatomy and grasping extremities (Martin 1968, 1990).

Most modern workers have focused on the grasping extremities and flattened nails, as well as branching of the carotid artery supply to the brain and of the formation of the auditory bulla of the cranium. In extant primates, the brain receives its blood supply via two principal routes (one pathway to the back of the brain and one toward the front). For all taxa, the paired vertebral arteries provide most of the blood to the back of the brain. Blood supply to the front, however, is more complex and involves branches of the internal carotid artery (ICA) and external carotid artery (ECA). For haplorhines (tarsiers, **catarrhines**, and **platyrrhines**), the main artery to the front of the brain is a branch of the ICA called the promontory artery (though most human gross anatomy textbooks simply refer to it as the internal carotid artery). In most lemuriforms, this is the job of a second branch of the ICA known as the stapedial artery (which tends to be absent in adult haplorhines). Finally, in lorisiformes and cheirogaleid lemuriformes, the front of the brain is supplied by the ascending pharyngeal artery (a branch of the ECA). These differences provide a valuable method for reconstructing phylogenetic relationships between fossil primates and living taxa.

In all extant primates, the auditory bulla is ossified and is formed by an extension of the petrous part of the temporal bone (or, more simply, petrosal bone). This last trait, a petrosal bulla, is perhaps the best candidate for a universally applicable diagnostic trait of primates. Unfortunately, it is often extremely difficult to assess in an adult cranium and perhaps even more difficult to assess in a fossil that has various cracks and deformities associated with preservation and preparation.

Although taxonomists crave neat and complete lists of traits to aid in sorting animals into bins, the true definition of a phylogenetic group is always one of descent from a common ancestor. The Order Primates is made up of all of the descendants of some common ancestor in the remote past. This last common ancestor probably did not possess all of the traits common to primates today and might have been indistinguishable from other primitive placental mammals living in the Cretaceous Period.

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2.2.2: Major Hypotheses About Primate Origins

For many groups of mammals, there is a key feature that led to their success. A good example is powered flight in bats. Primates lack a feature like this. Instead, if there is something unique about primates, it is probably a group of features rather than one single thing. Because of this, anthropologists and paleontologists struggle to describe an ecological scenario that could explain the rise and success of our own order. Three major hypotheses have been advanced to explain the origin of primates and to explain what makes our own order unique among mammals (Figure 8.1); these are described below.

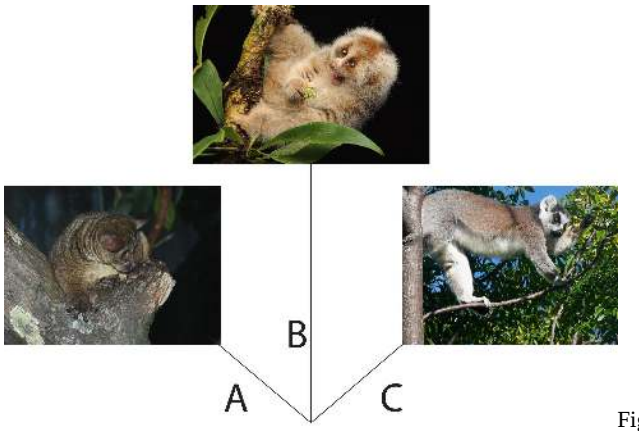


Figure 2.2.2.1: Three major hypotheses are A) the arboreal hypothesis, B) the visual predation hypothesis, and C) the angiosperm-primate coevolution hypothesis.

Arboreal Hypothesis

In the 1800s, many anthropologists viewed all animals in relation to humans. That is, animals that were more like humans were considered to be more “advanced” and those lacking humanlike features were considered more “primitive.” This way of thinking was particularly obvious in studies of primates.

Thus, when anthropologists sought features that separate primates from other mammals, they focused on features that were least developed in lemurs and lorises, more developed in monkeys, and most developed in apes (Figure 8.2). Frederic Wood Jones, one of the leading anatomist-anthropologists of the early 1900s, is usually credited with the Arboreal Hypothesis of primate origins (Jones 1916). This hypothesis holds that many of the features of primates evolved to improve locomotion in the trees. For example, the grasping hands and feet of primates are well suited to gripping tree branches of various sizes and our flexible joints are good for reorienting the extremities in many different ways. A mentor of Jones, Grafton Elliot Smith, had suggested that the reduced olfactory system, acute vision, and forward-facing eyes of primates are an adaptation to making accurate leaps and bounds through a complex, three-dimensional canopy (Smith 1912). The forward orientation of the eyes in primates causes the visual fields to overlap, enhancing depth perception, especially at close range. Evidence to support this hypothesis includes the facts that many extant primates are arboreal, and the primitive members of most primate groups are dedicated arborealists. The Arboreal Hypothesis was well accepted by most anthropologists at the time and for decades afterward.

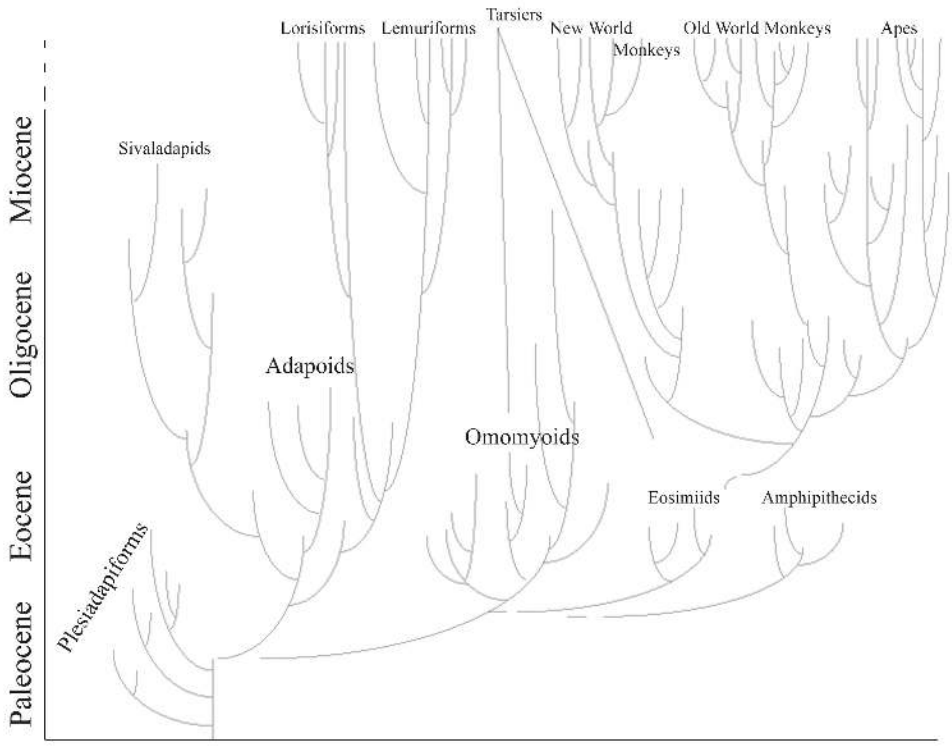


Figure 2.2.2.2: Primate family tree showing major groups. Disconnected lines show uncertainty about relationships. Note two lines leading to tarsiers from different possible groups of origin. The timescale is shortened for the epochs since the Miocene.

Visual Predation Hypothesis

In the late 1960s and early 1970s, Matt Cartmill studied and tested the idea that the characteristic features of primates evolved in the context of arboreal locomotion. Cartmill noted that squirrels climb trees (and even vertical walls) very effectively, even though they lack some of the key adaptations of primates. As members of the Order Rodentia, squirrels also lack the hand and foot anatomy of primates. They have claws instead of flattened nails and their eyes face more laterally than those of primates. Cartmill reasoned that there must be some other explanation for the unique traits of primates. He noted that some non-arboreal animals share at least some of these traits with primates; for example, cats and predatory birds have forward-facing eyes that enable visual field overlap. Cartmill suggested that the unique suite of features in primates is an adaptation to detecting insect prey and guiding the hands (or feet) to catch insects (Cartmill 1972). His hypothesis emphasizes the primary role of vision in prey detection and capture; it is explicitly comparative, relying on form function relationships in other mammals and nonmammalian vertebrates. According to Cartmill, many of the key features of primates evolved for preying on insects in this special manner (Cartmill 1974).

Angiosperm-Primate Coevolution Hypothesis

The visual predation hypothesis was unpopular with some anthropologists. One reason for this is that many primates today are not especially predatory. Another is that, whereas primates do seem well adapted to moving around in the smallest, terminal branches of trees, insects are not necessarily easier to find there. A counterargument to the visual predation hypothesis is the angiosperm-primate coevolution hypothesis. Primate ecologist Robert Sussman (Sussman 1991) argued that the few primates that eat mostly insects often catch their prey on the ground rather than in the fine branches of trees. Furthermore, predatory primates often use their ears more than their eyes to detect prey. Finally, most early primate fossils show signs of having been omnivorous rather than insectivorous. Instead, he argued, the earliest primates were probably seeking fruit. Fruit (and flowers) of angiosperms (flowering plants) often develop in the terminal branches. Therefore, any mammal trying to access those fruits must possess anatomical traits that allow them to maintain their hold on thin branches and avoid falling while reaching for the fruits. Primates likely evolved their distinctive visual traits and extremities in the Paleocene (approximately 65 million to 54 million years ago) and Eocene (approximately 54 million to 34 million years ago) epochs, just when angiosperms were going through a revolution of their own—the evolution of large, fleshy fruit that would have been attractive to a small arboreal mammal. Sussman argued that, just as primates were evolving anatomical traits that made them more efficient fruit foragers, angiosperms were also evolving fruit that would be more attractive to primates to promote better seed dispersal. This mutually beneficial relationship between the angiosperms and the primates was termed "coevolution" or more specifically "**diffuse coevolution**."

At about the same time, D. Tab Rasmussen noted several parallel traits in primates and the South American woolly opossum, *Caluromys*. He argued that early primates were probably foraging on both fruits and insects (Rasmussen 1990). As is true of *Caluromys* today, early primates probably foraged for fruits in the terminal branches of angiosperms, and they probably used their visual sense to aid in catching insects. Insects are also attracted to fruit (and flowers), so these insects represent a convenient opportunity for a primarily fruit-eating primate to gather protein. This solution is, in effect, a compromise between the visual predation hypothesis and the angiosperm-primate coevolution hypothesis. It is worth noting that other models of primate origins have been proposed, and these include the possibility that no single ecological scenario can account for the origin of primates.

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2.2.3: The Origin of Primates

Paleocene: Mammals in the Wake of Dinosaur Extinctions

Placental mammals, including primates, originated in the Mesozoic Era (approximately 251 million to 65.5 million years ago), the Age of Dinosaurs. During this time, most placental mammals were small, probably nocturnal, and probably avoided predators via camouflage and slow, quiet movement. It has been suggested that the success and diversity of the dinosaurs constituted a kind of ecological barrier to Mesozoic mammals. The extinction of the dinosaurs (and many other organisms) at the end of the Cretaceous Period (approximately 145.5–65.5 million years ago) might have opened up these ecological niches, leading to the increased diversity and disparity in mammals of the Tertiary Period (approximately 65.5–2.5 million years ago).

The Paleocene was the first epoch in the Age of Mammals. Soon after the Cretaceous-Tertiary (K-T) extinction event, new groups of placental mammals appear in the fossil record. Many of these groups achieved a broad range of sizes and lifestyles as well as a great number of species before declining sometime in the Eocene (or soon thereafter). These groups were ultimately replaced by the modern orders of placental mammals (Figure 8.3). It is unknown whether these replacements occurred gradually, for example by competitive exclusion, or rapidly, perhaps by sudden geographic dispersals with replacement. In some senses, the Paleocene might have been a time of recovery from the extinction event; it was cooler and more seasonal globally than the subsequent Eocene.



Figure 2.2.3.1: Depiction of Eocene flora and fauna in North America.

Plesiadapiforms, the Archaic Primates

The Paleocene epoch saw the emergence of several families of mammals that have been implicated in the origin of primates. These are the plesiadapiforms. Plesiadapiforms are archaic primates, meaning that they possessed some primate features and lacked others. The word *plesiadapiform* means “almost adapiform,” a reference to some similarities between some plesiadapiforms and some adapiforms (or adapoids; later-appearing true primates)—mainly in the molar teeth. Because enamel fossilizes better than other parts of the body, the molar teeth are the parts most often found and first discovered for any new species. Thus, dental similarities were often the first to be noticed by early mammalian paleontologists, partly explaining why plesiadapiforms were thought to be primates. Major morphological differences between plesidapiforms and euprimates (true primates) were observed later when more parts of plesiadapiform skeletons were discovered. Many plesiadapiforms have unusual anterior teeth and most have digits possessing claws rather than nails. So far, no plesiadapiform ever discovered has a postorbital bar (seen in extant strepsirrhines) or septum (as seen in **haplorhines**), and whether or not the **auditory bulla** was formed by the **petrous bone** remains unclear for many plesiadapiform specimens. Nevertheless, there are compelling reasons (partly from new skeletal material) for including plesidapiforms within the Order Primates.

Geographic and Temporal Distribution

Purgatorius is generally considered to be the earliest primate. This Paleocene mammal is known from teeth that are very primitive for a primate. It has some characteristics that suggest it is a basal plesiadapiform, but there is very little to link it specifically with euprimates (see Clemens 2004). Its ankle bones suggest a high degree of mobility, signaling an arboreal lifestyle (Chester et al. 2015). *Purgatorius* is primitive enough to have given rise to all primates, including the plesiadapiforms. Plesiadapiform families were numerous and diverse during parts of the Paleocene in western North America and western Europe, with some genera (e.g., *Plesiadapis*; see Table 8.1) living on both continents (Figure 8.4). Thus, there were probably corridors for plesiadapiform dispersal between the two continents, and it stands to reason that these mammals were living all across North America, including in the

eastern half of the continent and at high latitudes. A few plesiadapiforms have been described from Asia (e.g., *Carpocristes*), but the affinities of these remain uncertain.

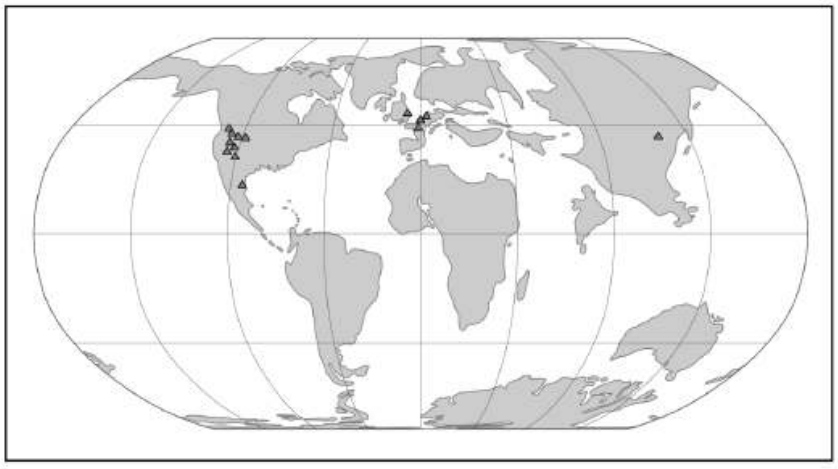


Figure 2.2.3.2: Map of the world in the Paleocene, highlighting plesiadapiform localities.

General Morphological Features

Although there is much morphological variation among the families of plesiadapiforms, there are some common features of the group. Most plesiadapiforms were small, the largest being about three kilograms (approximately 7 lbs.; *Plesiadapis cookei*). They had small brains and fairly large snouts, with variable eye size (as deduced from the bony orbits). In general, the eyes faced more laterally than in euprimates. Most plesiadapiforms have large incisors relative to the molars and in some species, the lower incisors (usually one pair) are reminiscent of long daggers or spears. In many plesiadapiforms, the upper central incisors are also very unusual, with small cuspules spaced out like fingers, having some unknown function perhaps related to seizing or cropping food. Many species show reduction and/or loss of the canine and anterior premolars, with the resulting formation of a rodent-like **diastema**; this probably implies a herbivorous diet. The spaces available for the chewing musculature are very large, and most plesiadapiforms probably had very powerful chewing muscles, perhaps capable of processing very tough foods (e.g., leaves). Some families appear to have had very specialized diets, as suggested by unusual tooth and jaw shapes. For example, an enlarged, laterally compressed, blade-like lower premolar appears to have evolved via **convergent evolution** in two different families, the Carpolestidae and the Saxonellidae.

Arguably the most interesting and unusual family of plesiadapiforms is the Carpolestidae. This family contains three major genera and a few minor ones. They are almost exclusively from North America (with a couple of possible members from Asia), and mainly from the Middle and Late Paleocene. Their molars are not very remarkable, being quite similar to those of some other plesiadapiforms (e.g., Plesiadapidae). However, nearly everything else is unusual. Their lower posterior premolars (p4) are laterally compressed and blade-like with vertical serrations topped by tiny cuspules. This unusual dental morphology is termed "**plagiaulacoid**" (Simpson 1933). It is similar to the condition in some living and fossil marsupials, but in marsupials, the blade-like lower tooth slides across a similar-looking blade-like upper tooth. In carpolestids, the blade-like tooth meets upper premolars that look completely different. The upper premolar occlusal surfaces are broad and are covered with many small cuspules; the blade-like lower premolar might have cut across these cuspules, between them, or both.



Figure 2.2.3.3: An artistic rendition of *Carpolestes simpsoni* moving along a small diameter support.

Many plesiadapiforms have hallmarks of arboreality in the skeleton, though the long bones are rather robust. Instead of having nails, most taxa had sharp claws on most or all of the digits. The extremities show signs that at least some of these archaic primates had grasping abilities comparable to those of primates and some arboreal marsupials. Nearly complete skeletons are known for several North American plesiadapiforms, and these have yielded a tremendous wealth of information on locomotor and foraging habits. Many plesiadapiforms appear to have been well adapted to clinging to vertical substrates (like a broad tree trunk) using their sharp claws, propelling themselves upward using powerful hindlimbs, bounding along horizontal supports, grasping smaller branches, and moving head-first down tree trunks. In carpolestids in particular, the skeleton appears to have been especially well adapted to moving slowly and carefully in small terminal branches. The big toe likely was especially good at grasping (Figure 8.5). There is a single specimen of a flattened nail-bearing distal big toe bone of *Carpolestes simpsoni* (Table 8.1), and this feature suggests affinities with euprimates.

Debate: Relationship of Plesiadapiforms to True Primates

In the middle of the 20th century, treeshrews (Order Scandentia) were often considered part of the Order Primates, based on anatomical similarities between some treeshrews and primates. For many people, plesiadapiforms represented intermediates between primates and treeshrews, so plesiadapiforms were included in Primates as well.

Later, studies of reproduction and brain anatomy in treeshrews and lemurs suggested that treeshrews are not primates (e.g., Martin 1968). This was soon followed by the suggestion to also expel plesiadapiforms (Martin 1972). Like treeshrews, plesiadapiforms lack a postorbital bar, nails, and details of the ear region that characterize true primates. Many paleoanthropologists were reluctant to accept this move to banish plesiadapiforms (e.g. P. D. Gingerich 1980).

Later, Beard (1990) found that in some ways, the digits of paromomyid plesiadapiforms are actually more similar to those of dermopterans (Order Dermoptera), the closest living relatives of primates, than they are to those of primates themselves (but see Krause 1991). At the same time, Kay and colleagues (1990) found that cranial circulation patterns and auditory bulla morphology in the paromomyid, *Ignacius* (Table 8.1), are more like those of dermopterans than like those of primates.

For many anthropologists, this one-two punch effectively removed plesiadapiforms from the Order Primates. In the last two decades, the tide of opinion has turned again, with many researchers including plesiadapiforms in the Order Primates. New and more complete specimens demonstrate that the postcranial skeletons of plesiadapiforms, including the hands and feet, were primate-like, not dermorpteran-like (Bloch and Boyer 2002, 2007). New fine-grained CT scans of relatively complete plesiadapiform skulls revealed that they share some key traits with primates to the exclusion of other placental mammals (Bloch and Silcox 2006). Most significant was the suggestion that *Carpolestes simpsoni* possessed an auditory bulla formed by the petrosal bone, like in all living primates.

The debate about the status of plesiadapiforms continues, owing to a persistent lack of key bones in some species and owing to genuine complexity of the anatomical traits involved. Maybe plesiadapiforms were the primitive stock from which all primates arose, with some plesiadapiforms (e.g., carpolestids) nearer to the primate **stem** than others.

Geographic and Temporal Distribution

The first universally accepted primates to appear in the fossil record are the earliest members of two groups: the adapoids and the omomyoids. These groups become quite distinct over evolutionary time, filling mutually exclusive niches for the most part. However, at the start of the Eocene, the most primitive adapoids are very similar to the most primitive omomyoids.

Adapoids are called adapiforms or adapids by some and are here considered members of the superfamily **Adapoidea**. Omomyoids (omomyiforms or omomyids, according to some) are members of the superfamily **Omomyoidea**. The adapoids were mainly diurnal and herbivorous, with some achieving larger sizes than any plesiadapiforms (10 kg; 22 lbs.). By contrast, the omomyoids were mainly nocturnal, insectivorous and frugivorous, and small.

Both groups appear suddenly at the start of the Eocene, where they are present in western North America, western Europe, and India (Figure 8.6). If the primate *Altiatlasius* is an omomyoid, then these were also present in the Late Paleocene of North Africa. This wide dispersal of early primates was probably due to the presence of rainforest corridors extending far into northern latitudes.

In North America and Europe, both groups achieved considerable diversity in the Middle Eocene, then mostly died out at the end of that epoch. In some Eocene rock formations in the western United States, adapoids and omomyoids make up a major part of the mammalian fauna. The Eocene of India has yielded a modest diversity of euprimates, some of which are so primitive that it is difficult to know whether they are adapoids or omomyoids (or even early anthropoids).

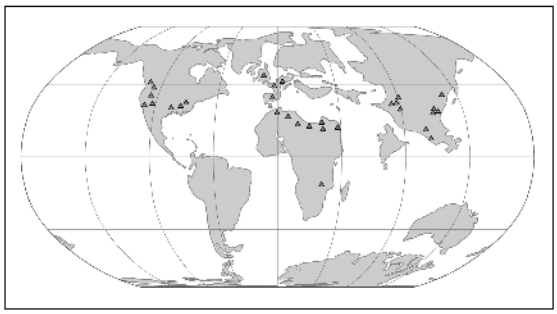


Figure 2.2.3.4: Map of the world in the Eocene, highlighting adapoid and omomyoid localities.

Adapoids and omomyoids barely survived the Eocene-Oligocene extinctions, when colder temperatures, increased seasonality, and the retreat of rainforests to lower latitudes led to changes in mammalian biogeography. In North America, one genus originally considered an omomyoid but recently placed in the Adapoidea persisted until the Miocene: *Ekgmowechashala*, from various parts of North America (Rose and Rensberger 1983). This taxon has highly unusual teeth and might have been a late immigrant to North America from Asia. In Asia, one family of adapoids, the Sivaladapidae, retained considerable diversity as late as the Late Miocene. In Africa and Arabia, several fossil primates resembling extant strepsirrhines were present in the Eocene and Oligocene (approximately 34 million to 24 million years ago; Seiffert 2012).

Adapoid Diversity

Adapoids were very diverse, particularly in the Eocene of North America and Europe. They can be divided into six families, with a few species of uncertain familial relationship. As a group, adapoids have some features in common, although much of what they share is primitive. Important features include the hallmarks of euprimates: postorbital bar, flattened nails, grasping extremities, and a petrosal bulla. In addition, some adapoids retain the primitive dental formula of 2.1.4.3; that is, in each quadrant of the mouth, there are two incisors, one canine, four premolars, and three molars. In general, the incisors are small compared to the molars, but the canines are relatively large, with sexual dimorphism in some species. Their snouts are somewhat long, and evidence from cranial specimens suggests that the carotid artery branches that fed the front of the brain were variable and sometimes multiple. Cutting crests on the molars are well developed in some species, and the two halves of the mandible were fused at the midline in some species. Some adapoids were quite small (*Anchomomys* at a little over 100 g), and some were quite large (*Magnadapis* at 10 kg; 22 lbs.). Many had relatively small eyes, and in some the eyes faced somewhat laterally and/or upwardly. Furthermore, the spaces and attachment features for the chewing muscles were truly enormous in some species, suggesting that these muscles were very large and powerful. Taken together, this suggests an overall adaptive profile of diurnal herbivory. The canine sexual dimorphism in some species suggests a possible mating pattern of polygyny, as males in polygynous primate species often compete with each other for mates and have especially large canine teeth. The description that follows provides greater detail for the two best known adapoid families, the Adapidae and the Notharctidae; the additional families are summarized briefly.

The first adapoids to be described belong to the family Adapidae. This family was exclusive to Europe and includes some of the most cranially and postcranially robust primates of the Eocene (Figure 8.7). The first primate fossil ever named was *Adapis*, which was described by Baron Georges Cuvier between 1812 and 1822. Originally it was thought to be an ungulate and was recognized as a primate starting in the 1870s. Many adapids are known from exceptionally complete cranial and postcranial material from France and Switzerland. Unfortunately, most of the best fossils were collected in the 1800s as part of fertilizer mining operations and stratigraphic provenience of those specimens is uncertain. Furthermore, these fossils come from jumbled fissure fills, making it hard to know which bones came from the same animal.



Figure 2.2.3.5: Representative crania of adapids (European adapoids) from the natural history museum in Montauban, France. The white scale bar is 1 cm long.

Perhaps the best known adapoids are the Notharctidae from western North America, with a few species from Europe. Collections from Wyoming and Colorado in the United States have yielded many relatively complete skeletons—not to mention thousands of jaws with teeth—of such genera as *Notharctus* (Table 8.1), *Cantius*, and *Smilodectes*. The notharctids have been described as especially lemur-like (Table 8.2) on the basis of their postcranial adaptations for clinging and leaping as well as on the basis of overall cranial resemblance (Gregory 1920). The primitive *Cantius* has representatives in both North America and Europe.

The Cercamoniidae (e.g., *Donrussellia*; Table 8.1) from Europe and Asia includes some of the most primitive adapoids. The Caenopithecidae contains several genera once considered to be in Cercamoniidae, but that share an overall decrease in the length of the snout accompanied by increasing robusticity of the jaws, loss of some premolar teeth, and leaping adaptations. This family must have been very widely dispersed across the northern continents as it has representatives in the Eocene of Europe, North America, Africa, and Asia (Kirk and Williams 2011; Seiffert et al. 2009). It includes the Fayum genera *Aframonius* and *Afradapis* (Table 8.1) as well as *Europolemur*, *Godinotia*, and *Darwinius* (Figure 8.8) from the Messel oil shales in Germany (approximately 47.3 million years ago).



Figure 2.2.3.6: Darwinius masillae. The slab on the left is Plate A and the slab on the right is Plate B. The parts of the skeleton in B that are outside of the dashed lines were fabricated.

The Asiadapidae and Sivaladapidae are known from only Asia. Asiadapids are primitive adapoids from India. Postcranial elements are known from the same horizons as the described teeth, but the combination of anatomical traits in these bones makes it difficult to know if they belonged to adapoids or to omomyoids, both of which were present (Dunn et al. 2016; Rose et al. 2018). The Sivaladapidae from India, Pakistan, China, and Thailand (e.g., *Sivaladapis*; Table 8.1), mostly represented by jaws with teeth, persisted well into the Miocene and, in some cases, achieved a large size (4 kg; 8.82 lbs.). The sivaladapids might have evolved from the asiadapids.

Omomyoid Diversity

Like adapoids, omomyoids appeared suddenly at the start of the Eocene and then became very diverse with most species dying out before the Oligocene. Omomyoids are known from thousands of jaws with teeth, relatively complete skulls for about a half-dozen species, and very little postcranial material. Omomyoids were relatively small primates, with the largest being less than three kilograms (approximately 7 lbs.; *Macrotarsiusmontanus*). All known crania possess a postorbital bar, which in some has been described as “incipient closure.” Some—but not all—known crania have an elongated bony ear tube extending lateral to the location of the eardrum, a feature seen in living tarsiers and catarrhines. The anterior teeth tend to be large, with canines that are usually not much larger than the incisors. Often it is difficult to distinguish closely related species using molar morphology, but the premolars tend to be distinct from one species to another. The postcranial skeleton of most omomyoids shows hallmarks of leaping behavior reminiscent of that of tarsiers.

European omomyoids are grouped together in one family, the Microchoeridae. All microchoerids were small, had relatively large eyes, and were probably nocturnal frugivore-insectivores. Some species are known from some of the same classic fissure fill deposits as adapoids. These have yielded beautifully preserved cranial material, especially for the genus *Necrolemur*. The cranial morphology of *Necrolemur* led early paleoanthropologists to suspect they had something to do with the origin of tarsiers, a hypothesis that persists to this day (see Table 8.2). Furthermore, well-preserved ankle bones of *Necrolemur* and other microchoerids are strikingly like the ankle bones of tarsiers (Schmid 1979), suggesting that if there is no special relationship to tarsiers, then at least they were leaping in very similar ways. In North America, omomyoids became very diverse and abundant. In fact, omomyoids from Wyoming are sufficiently abundant and from such stratigraphically controlled conditions that they have served as strong evidence for the gradual evolution of anatomical traits over time (Rose and Bown 1984). These gradual changes have also made it difficult in some cases to establish clear boundaries between species because such boundaries usually rely on discrete differences in anatomical traits. As with European omomyoids, those in North America were probably mainly small, nocturnal, and frugivorous-insectivorous (Strait 2001). The preserved crania in some species (e.g., *Shoshonius*) are very like those of tarsiers (Beard and MacPhee 1994), though lacking the degree of postorbital closure. Crania in some other species (e.g., *Rooneyia*) are quite unusual.

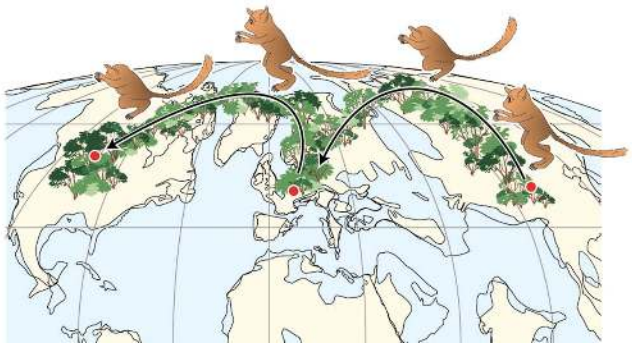


Figure 2.2.3.7: A map of the world during the earliest Eocene showing one hypothesis for the direction of dispersal of the omomyoid *Teilhardina*. The image also emphasizes the presence of forest corridors at high latitudes. Smith et al. 2006. Copyright (2006) National Academy of Sciences.

North American omomyoids are grouped into one family, Omomyidae, with two subfamilies: Anaptomorphinae and Omomyinae. The anaptomorphines were mostly smaller and more generalized whereas some omomyines achieved larger sizes (1–2 kg; 2–4 lbs.) and some were more specialized.

Teilhardina (Figure 8.9; Table 8.1) is one of the earliest and arguably the most primitive of omomyoids. *Teilhardina* has several species, most of which are from North America, with one from Europe (*T. belgica*) and one from Asia (*T. asiatica*). The species of this genus are anatomically similar and the deposits from which they are derived are roughly contemporaneous. Thus, this small primate likely dispersed across the northern continents very rapidly (Smith et al. 2006).

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2.2.4: The Emergence of Modern Primate Groups

Origins of Crown Strepsirrhines

Until the turn of this century, very little was known about the origins of the crown (living) strepsirrhines. The Quaternary record of Madagascar contains many amazing forms of lemurs, including giant sloth-like lemurs, lemurs with perhaps monkey-like habits, lemurs with koala-like habits, and even a giant aye-aye (Godfrey and Jungers 2002). However, in Madagascar early Tertiary continental sediments are lacking, and there is no record of lemur fossils before the Pleistocene.

The fossil record of galagos is slightly more informative. Namely, there are Miocene African fossils that are very likely progenitors of lorisids (Simpson 1967). However, these are much like modern galagos and do not reveal anything about the relationship between crown strepsirrhines and Eocene fossil primates (but see below regarding *Propotto*). A similar situation exists for lorises in Asia: there are Miocene representatives, but these are substantially like modern lorises.

In 2003, the description of two new fossil genera from the Birket Qarun locality in the Fayum Basin of Egypt provided the "smoking gun" for the origin of crown strepsirrhines (Seiffert et al. 2003). *Saharagalago* and *Karanisia* are two small primates that bear clear affinities with crown strepsirrhines to the exclusion of other primates. Most striking is a lower canine of *Karanisia* that clearly sat within a strepsirrhine-style **toothcomb**. Recently, several other African primates have been recognized as having strepsirrhine affinities (Seiffert 2012). These include *Azibius* and *Algeripithecus* from Algeria, *Djebelemur* from Tunisia, *Omanodon* and *Shizarodon* from Oman, and *Namaia* from Namibia (see Marivaux et al. 2013). These important fossil primates are mainly known from teeth and jaws. The enigmatic Fayum primate *Plesiopithecus* is known from a single skull that has been compared to aye-ayes and to lorises (Godinot 2006; Simons and Rasmussen 1994a).

The now-recognized diversity of stem strepsirrhines from the Eocene and Oligocene of Afro-Arabia is strong evidence to suggest that strepsirrhines originated in that geographic area. This implies that lorises dispersed to Asia subsequent to an African origin. It is unknown what the first strepsirrhines in Madagascar were like. However, it seems likely that the lemuriform-lorisiform split occurred in continental Africa, followed by dispersal of lemuriform stock to Madagascar. Recent evidence suggests that *Propotto*, a Miocene primate from Kenya originally described as a potto antecedent, actually forms a clade with *Plesiopithecus* and the aye-aye; this might suggest that strepsirrhines dispersed to Madagascar from continental Africa more than once (Gunnell et al. 2018).

The Fossil Record of Tarsiers

Tarsiers are so unusual that they fuel major debates about primate taxonomy. Tarsiers today are moderately diverse but geographically limited and not very different in their ecological habits—especially considering that the split between them and their nearest living relative probably occurred over 50 million years ago. If omomyoids are excluded, then the fossil record of tarsiers is very limited. Two fossil species from the Miocene of Thailand have been placed in the genus *Tarsius*, as has an Eocene fossil from China (Beard et al. 1994). These, and *Xanthorhysis* from the Eocene of China, are all very tarsier-like. In fact, it is striking that *Tarsius eocaenus* from China was already so tarsier-like as early as the Eocene. This suggests that tarsiers achieved their current morphology very early on in their evolution and have remained more or less the same while other primates changed dramatically. Two additional genera, *Afrotarsius* from the Oligocene of Egypt and Libya and *Afrasia* from the Eocene of Myanmar, have also been implicated in tarsier origins, though the relationship between them and tarsiers is unclear (Chaimanee et al. 2012). More recently, a partial skeleton of a small Eocene primate from China, *Archicebus achilles* (dated to approximately 55.8 million to 54.8 million years ago), was described as the most basal tarsiiform (Ni et al. 2013). This primate is reconstructed as a diurnal insectivore and an arboreal quadruped that did some leaping—but not to the specialized degree seen in living tarsiers. The anatomy of the eye in living tarsiers suggests that their lineage passed through a diurnal stage, so *Archicebus* (and diurnal omomyoids) might represent such a stage.

Climate Change and the Paleogeography of Modern Primate Origins

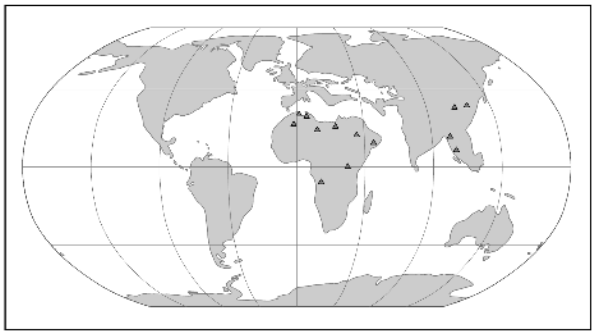


Figure 2.2.4.1: Map of key localities of early anthropoids. Note that the landmasses are in their current configuration.

Changing global climate has had profound effects on primate dispersal patterns and ecological habits over evolutionary time. Primates today are strongly tied to patches of trees and particular plant parts such as fruits, seeds, and immature leaves. It is no surprise, then, that the distribution of primates mirrors the distribution of forests. Today, primates are most diverse in the tropics and especially in tropical rainforests. Global temperature trends across the Tertiary have affected primate ranges. Following the Cretaceous-Tertiary extinction event, cooler temperatures and greater seasonality characterized the Paleocene. In the Eocene, temperatures (and probably rainfall) increased globally and rainforests likely extended to very high latitudes. During this time, euprimates became very diverse. With cooling and increased aridity at the end of the Eocene, many primate extinctions occurred in the northern continents and the surviving primates were confined to lower latitudes in South America, Afro-Arabia, Asia, and southern Europe. Among these survivors are the progenitors of the living groups of primates: lemurs and lorises, tarsiers, New World monkeys, Old World monkeys, and apes (Figure 8.10).

Competing Hypotheses for the Origin of Anthropoids

There is considerable debate among paleoanthropologists as to the geographic origins of anthropoids. In addition, there is debate regarding the source group for anthropoids. Three different hypotheses have been articulated in the literature. These are the adapoid origin hypothesis, the omomyoid origin hypothesis, and the tarsier origin hypothesis (Figure 2.2.4.2).

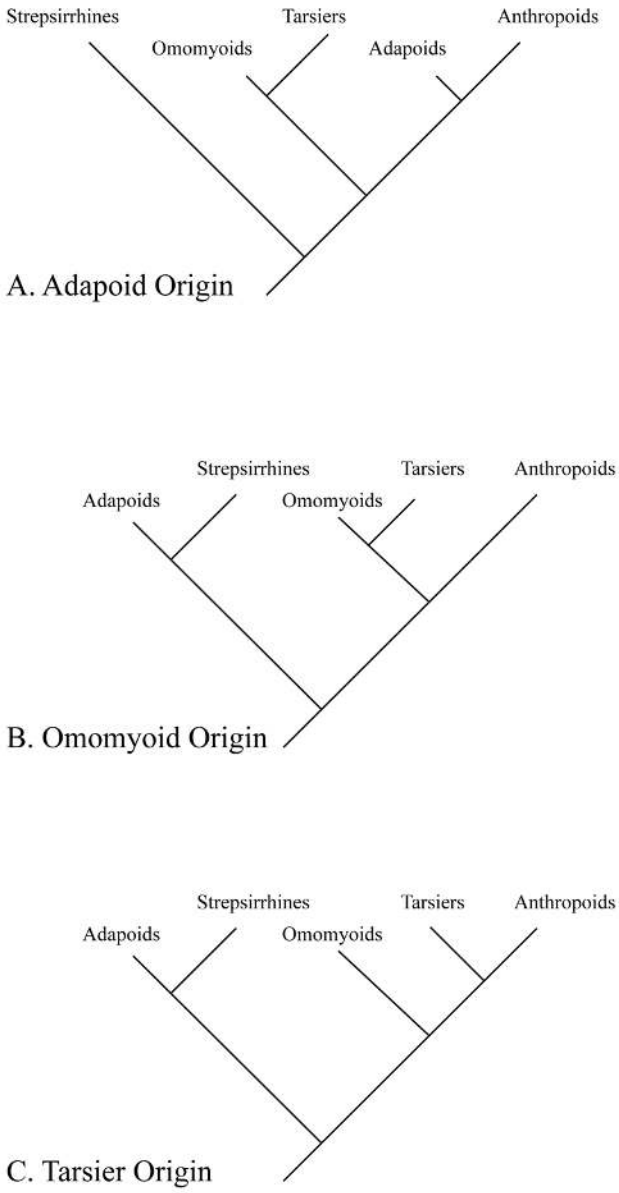


Figure 2.2.4.2: Competing trees for anthropoid origins. Branch lengths are not to scale. Note that the position of strepsirrhines is not necessarily specified by the omomyoid origin and tarsier origin models.

Adapoid Origin Hypothesis

Resemblances between some adapoids and some extant anthropoids include fusion of the **mandibular symphysis**, overall robusticity of the chewing system, overall large body size, features that signal a diurnal lifestyle (like relatively small eye sockets), and details of ankle bone morphology. Another feature in common is canine sexual dimorphism, which is present in some species of adapoids (probably) and in several species of anthropoids.

These features led some paleoanthropologists in the last half of the 20th century to suggest that anthropoids arose from adapoid stock (Gingerich 1980; Simons and Rasmussen 1994b). One of the earliest supporters of the link between adapoids and anthropoids was Hans Georg Stehlin, who described much of the best material of adapoids and who compared these Eocene primates to South American monkeys (Stehlin 1912). In more recent times, the adapoid origin hypothesis was reinforced by resemblances between these European adapoids (especially *Adapis* and *Leptadapis*) and some early anthropoids from the Fayum Basin (e.g., *Aegyptopithecus*, see below; Table 8.1).

Unfortunately for the adapoid hypothesis, most of the shared features listed above probably arose independently in the two groups as adaptations to a diet of hard and/or tough foods. For example, fusion of the mandibular symphysis likely evolved as a means to strengthen the jaw against forces that would pull the two halves away from each other, in the context of active chewing muscles on both sides of the head generating great bite forces. This context would also favor the development of robust jaws, large chewing muscles, shorter faces, and some other features shared by some adapoids and some anthropoids.

As older and more primitive anthropoids were found in the Fayum Basin, it became clear that the earliest anthropoids from Africa do not possess these features of jaw robusticity (Seiffert et al. 2009). Furthermore, many adapoids never evolved these features. Fusion of the mandibular symphysis in adapoids is actually quite different from that in anthropoids and probably occurred during juvenile development in the former (Beecher 1983; Ravosa 1996). Eventually, the adapoid origin hypothesis fell out of favor among most paleoanthropologists, although the description of *Darwinius* is a recent revival of that idea (Franzen et al. 2009; but see Seiffert et al. 2009, Williams et al. 2010b).

Omomyoid Origin Hypothesis

Similarities in cranial and hindlimb morphology between some omomyoids and extant tarsiers have led to the suggestion that tarsiers arose from some kind of omomyoid. In particular, *Necrolemur* has many features in common with tarsiers, as does the North American *Shoshonius*, which is known from a few beautifully preserved (although distorted) crania. Tarsiers and *Shoshonius* share exclusively some features of the base of the cranium; however, *Shoshonius* does not have any sign of postorbital closure and it lacks the bony ear tube of tarsiers. Nevertheless, some of the resemblances between some omomyoids and tarsiers suggest that tarsiers might have originated from within the Omomyoidea (Beard 2002; Beard and MacPhee 1994). In this scenario, although living tarsiers and living anthropoids might be sister taxa, they might have evolved from different omomyoids, possibly separated from each other by more than 50 million years of evolution, or anthropoids evolved from some non-omomyoid fossil group. The arguments against the omomyoid origin hypothesis are essentially the arguments *for* the tarsier origin hypothesis (see below). Namely, tarsiers and anthropoids share many features (especially of the soft tissues) that must have been retained for many millions of years or must have evolved convergently in the two groups. Furthermore, a key hard-tissue feature shared between the two extant groups, the postorbital septum, was not present in any omomyoid. Therefore, that feature must have arisen convergently in the two extant groups or must have been lost in omomyoids. Neither scenario is very appealing, although recent arguments for convergent evolution of the postorbital septum in tarsiers and anthropoids have arisen from embryology and histology of the structure (DeLeon et al. 2016).

Tarsier Origin Hypothesis

Several paleoanthropologists have suggested that there is a relationship between tarsiers and anthropoids to the exclusion of omomyoids and adapoids (e.g., Cartmill and Kay 1978; Ross 2000; Williams and Kay 1995). As mentioned, tarsiers and anthropoids today share several traits. These include many soft-tissue features related to the olfactory system such as the loss of a hairless external nose and loss of the median cleft running from the nose to the mouth (possessed by strepsirrhines). Also included are aspects of the visual system such as the loss of a reflective layer at the back of the eye, similarities in carotid circulation to the brain, and mode of placentation. Unfortunately, none of these can be assessed directly in fossils. Some bony similarities between tarsiers and anthropoids include an extra air-filled chamber below the middle ear cavity, reduced bones within the nasal cavity, and substantial postorbital closure; these can be assessed in fossils, but the distribution of these traits in omomyoids does not yield clear answers. Furthermore, several of the similarities between tarsiers and anthropoids are probably due to similarities in the sensory

systems, which might have evolved in parallel for ecological reasons. Although early attempts to resolve the crown primates with molecular data were sometimes equivocal or in disagreement with one another, more recent analyses (including those of short interspersed elements) suggest that tarsiers and anthropoids are sister groups to the exclusion of lemurs and lorises (Williams et al. 2010a). However, this does not address omomyoids, all of which are far too ancient for DNA extraction.

The above three hypotheses are not the only possibilities for anthropoid origins. It may be that anthropoids are neither the closest sister group of tarsiers, nor evolved from adapoids or omomyoids. In recent years, two new groups of Eocene Asian primates have been implicated in the origin of anthropoids: the eosimiids and the amphipithecids. It is possible that one or the other of these two groups gave rise to anthropoids. Regardless of the true configuration of the tree for crown primates, the three major extant groups probably diverged from each other quite long ago (Seiffert et al. 2004).

Early Anthropoid Fossils in Africa

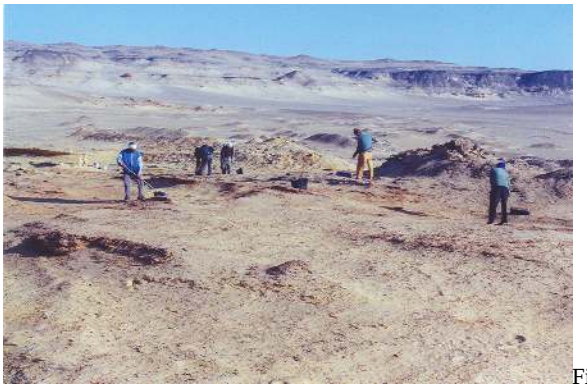


Figure 2.2.4.3: Egyptian workers sweeping Quarry I in the Fayum Basin (2004). This is a technique called wind harvesting that removes the desert crust and permits wind to blow out fine sediment and reveal fossils.



Figure 2.2.4.4: Elwyn Laverne Simons excavating *Aegyptopithecus* in the Fayum Basin.

The classic localities yielding the greatest wealth of early anthropoid fossils are those from the Fayum Basin in Egypt (Simons 2008; Figure 8.12). The Fayum is a veritable oasis of fossil primates in an otherwise rather spotty early Tertiary African record. Since the 1960s, teams led by E. L. Simons have discovered several new species of early anthropoids, some of which are known from many parts of the skeleton and several individuals (Figure 8.13).

The Fayum Jebel Qatrani Formation and Birket Qarun Formation between them have yielded a remarkable array of terrestrial, arboreal, and aquatic mammals. These include ungulates, bats, sea cows, elephants, hyraces, rodents, whales, and primates. Also, many other vertebrates, like water birds, were present. The area at the time of deposition (Late Eocene through Early Oligocene) was probably very wet, with slow-moving rivers, standing water, swampy conditions, and lots of trees (see Bown and Kraus 1988). In short, it was an excellent place for primates.

General Morphology of Anthropoids

The anthropoids known from the Fayum (and their close relatives from elsewhere in East Africa and Afro-Arabia) bear many of the anatomical hallmarks of extant anthropoids; however, there are primitive forms in several families that lack one or more anthropoid traits. All Fayum anthropoids known from skulls possess postorbital closure, most had fused mandibular symphyses, and most had ring-like **ectotympanic** bones. Tooth formulae were generally either 2.1.3.3 or 2.1.2.3. Fayum anthropoids ranged in size from the very small *Qatrania* and *Biretia* (less than 500 g) to the much-larger *Aegyptopithecus* (approximately 7 kg; 15 lbs.). Fruit was probably the main component of the diet for most or all of the anthropoids, with some of them supplementing with leaves (Kay and Simons 1980; Teaford et al. 1996; Kirk and Simons 2001). Most Fayum anthropoids were probably diurnal above-branch

quadrupeds. Some of them (e.g., *Apidium*; Table 8.1) were probably very good leapers (Gebo and Simons 1987), but none show specializations for gibbon-style suspensory locomotion. Some of the Fayum anthropoids are known from hundreds of individuals, permitting the assessment of individual variation, sexual dimorphism, and in some cases growth and development. The description that follows provides greater detail for the two best known Fayum anthropoid families, the Propliopithecidae and the Parapithecidae; the additional families are summarized briefly.

Fayum Anthropoid Families

The Propliopithecidae (e.g., *Pliopithecus*; Table 8.1) include the largest anthropoids from the fauna, and they are known from several crania and some postcranial elements. They have been suggested to be stem catarrhines (Old World Monkeys and apes), although perhaps near the split between catarrhines and platyrrhines. The best known propliopithecid is *Aegyptopithecus*, known from many teeth, crania, and postcranial elements. The crania (Figure 8.14) show substantial morphological variation between individuals, some of which might be due to sexual dimorphism and a polygynous mating system (Simons et al. 2007). *Aegyptopithecus* was large (greater than 7 kg; 15 lbs.) with prominent attachments for the chewing muscles and with low, rounded, and well-buttressed molars. The snout is long and the canines are large. There is only partial development of a bony ear tube (Simons et al. 2007). The known long bones of *Aegyptopithecus* are quite robust, and the skeleton suggests that this animal was a generalized arboreal quadruped with no strong specialization for suspension (Gebo and Simons 1987).



Figure 2.2.4.5: Female and male skull material for *Aegyptopithecus zeuxis*. The female is on the left. The mandibles are not associated with the crania. Simons et al. 2007. Copyright (2007) National Academy of Sciences.

An extremely abundant and unusual family of anthropoids from the Fayum is the Parapithecidae. Parapithecids have the primitive anthropoid tooth formula of 2.1.3.3 and they have very large conules on the upper molars and premolars. The parapithecid *Apidium* is known from many jaws with teeth, crushed and distorted crania, and several skeletal elements. The molars of *Apidium* had low, rounded cusps and thick enamel, suggesting a frugivorous diet. *Apidium* was probably a good leaper, having tightly apposed distal tibia and fibula as well as a narrow distal femur with a deep patellar groove (Fleagle and Simons 1995). *Parapithecus* is known from cranial material including a beautiful, undistorted cranium. This genus shows extreme reduction of the incisors, including complete absence of the lower incisors in *P. grangeri* (Simons 2001). This trait is unique among primates. *Biretia* is a primitive member of the family that has the primitive trait of an unfused mandibular symphysis. Parapithecids were once thought to be the ancestral stock of platyrrhines; however, their platyrrhine-like features are probably just primitive retentions and the most conservative approach is to consider them stem anthropoids.

The Oligopithecidae share the catarrhine tooth formula of 2.1.2.3 as well as having a canine honing complex that involves the anterior lower premolar. The postcranial elements known for the group suggest generalized arboreal quadrupedalism. The best known member, *Catopithecus*, is known from crania that demonstrate a postorbital septum and from mandibles that lack symphyseal fusion (Simons and Rasmussen 1996). The jaws are deep, with broad muscle attachment areas and crested teeth. *Catopithecus* was probably a little less than a kilogram in weight.

The Proteopithecidae had an overall primitive dentition that includes three premolars per quadrant and a generalized skeleton; they are considered stem anthropoids. The best known genus, *Proteopithecus*, is represented by dentitions, crania, and postcranial elements that suggest a diet of mostly fruit and a generalized style of locomotion, including arboreal quadrupedalism with some leaping (Simons and Seiffert 1999). It weighed about a kilogram.

Other genera of putative anthropoids from the Fayum include the very poorly known *Arsinoea*, the contentious *Afrotarsius*, and the enigmatic *Nosmips*. The last of these possesses traits of several major primate **clades** and defies classification (Seiffert et al. 2010).

Early Anthropoid Fossils in Asia

For the last half of the 1900s, researchers believed that Africa was the unquestioned homeland of early anthropoids (see Fleagle and Kay 1994). However, two very different groups of primates from Asia soon began to change that. One was an entirely new discovery (Eosimiidae), and the other was a poorly known group discovered decades prior (Amphipithecidae). Soon, attention on anthropoid origins began to shift eastward (see Ross and Kay 2004, Simons 2004). If anthropoids arose in Asia instead of Africa, then this implies that the African early anthropoids either emigrated from Asia or evolved their anthropoid traits in parallel with living anthropoids.

Eosimiids



Figure 2.2.4.6: Cast of the right half of the mandible of *Eosimias centennicus*, type specimen. The white scale bar is 1 cm long.

First described in the 1990s, the eosimiids are best represented by *Eosimias* (Table 8.1). This “dawn monkey” is known from relatively complete jaws with teeth, a few small fragments of the face, and some postcranial elements (Beard et al. 1994; Beard et al. 1996; Gebo et al. 2000). The lower jaw is distinctive in being very deep relative to its length and breadth, as in some early Fayum anthropoids (Figure 8.15). It also has pointed incisors that are about the same size as the canines. The lower premolars are crowded together and they are set obliquely in the jaw. This last trait, also present in another eosimiid called *Bahinia*, was described as a shared derived trait with anthropoids, though it is also present in some adapoids (e.g., *Afradapis* from North Africa and *Asiadapis* [Table 8.1] from India). The mandibular symphysis is vertically inclined, as in some anthropoids, but is unfused. Overall, *Eosimias* was small, no heavier than a can of soda pop. *Eosimias* (along with the other less-well-known genera in its family) bears some resemblance to tarsiers as well as anthropoids. The shared features with anthropoids are mainly jaw shape and details of dental morphology. Unfortunately, no good crania are known for this family and the anatomy of, for example, the posterior orbital margin could be very revealing as to higher-level relationships.

Amphipithecids

Amphipithecids are small- to medium-size primates (up to 10 kg; 22 lbs.). Most are from the Eocene Pondaung Formation in Myanmar (Early–Middle Eocene), but one genus is known from Thailand. They were first discovered in the 1910s, and all of the specimens discovered in the first half of the 20th century were fragmentary jaws with teeth that were mostly worn down. Nevertheless, some dental similarities with anthropoids were noted early on. These include deep jaws and wide basins that separate low molar cusps. Starting in the 1970s, intensive collecting efforts in Myanmar yielded new material for the best known genera *Pondaungia* and *Amphipithecus* (Ciochon and Gunnell 2002; Table 8.1). Soon, another genus was discovered: *Myanmarpithecus*. It bears some resemblance to the other genera but has longer molar crests, suggesting a higher degree of folivory (Kay et al. 2004). Another amphipithecid, *Siamopithecus* from Thailand, has very rounded molars and was probably a seed-eater (Figure 8.16). In addition to teeth and jaws, some cranial fragments, ankle material, and ends of postcranial bones have been found for *Pondaungia*. There are important resemblances between the postcranial bones of *Pondaungia* and those of adapoids, suggesting adapoid affinities for the amphipithecidae. This would imply that the resemblances with anthropoids in the teeth are convergent, based on similarities in diet (see Ciochon and Gunnell 2002). Unfortunately, the association between postcranial bones and teeth is not definite. With other primates in these faunas (including eosimiids), one cannot be certain that the postcranial bones belong with the teeth. Perhaps, as suggested by some, some of the bones belong to a sivaladapid (or asiadapid) and others belong to an early anthropoid (Beard et al. 2007; Marivaux et al. 2003). Additional well-associated material of amphipithecids would help to clear up this uncertainty.



Figure 2.2.4.7: Casts of representative amphipithecid material. A, *Pondaungia cotteri* right lower jaw fragment with m2 and m3. B, *Siamopithecus eocaenus* right upper jaw fragment with p4-m3. C, *S. eocaenus* right lower jaw fragment with partial m1, m2, and m3 in lateral view; note the great depth of this jaw. D, same as in C, but occlusal view. White scale bars are 1 cm long; the scale is the same for A, B, and D.

Platyrrhine Dispersal to South America

Today there is an impressive diversity of primates in South and Central America. These are considered to be part of a single clade, the Platyrrhini. Primates colonized South America sometime in the Eocene from an African source. In the first half of the 20th century, the source of platyrrhines was a matter of major debate among paleontologists, with some favoring a North American origin (e.g., Simpson 1940).

Part of the reason for this debate is that South America was an island in the Eocene. Primates needed to cross open ocean to get there from either North America or Africa, although the distance from the former was shorter. Morphology yields clues to platyrrhine origins. The first known primates in South America have more in common morphologically with African primates than with North American ones. At the time, anthropoids were popping up in North Africa, whereas the only euprimates in North America were adapoids and omomyoids. Despite lacking a bony ear tube, early platyrrhines shared a great deal with other anthropoids, including full postorbital closure and fusion of the mandibular symphysis.

The means by which a population of small North African primates managed to disperse across the Atlantic and survive to colonize South America remains a mystery. The most plausible scenario is one of rafting. That is, primates must have been trapped on vegetation that was blown out to sea by a storm. The vegetation then became a sort of life raft, which eventually landed ashore, dumping its passengers in South America. Rodents probably arrived in South America in the same way (Antoine et al. 2012).

Once ashore, platyrrhines must have crossed South America fairly rapidly because the earliest-known primates from that continent are from Peru (Bond et al. 2015). Soon after that, platyrrhines were in Bolivia, namely *Branisella*. By the Miocene, platyrrhines were living in extreme southern Argentina and were exploiting a variety of feeding niches. The Early Miocene platyrrhines were all somewhat primitive in their morphology, but some features that likely arose by ecological convergence suggest (to some) relationships with extant platyrrhine families. This has led to a lively debate about the pattern of primate evolution in South America (Kay 2015; Kay and Fleagle 2010; Rosenberger 2010). By the Middle Miocene, clear representatives of modern families were present in a diverse fauna from La Venta, Colombia (Wheeler 2010). The Plio-Pleistocene saw the emergence of giant platyrrhines as well as several taxa of platyrrhines living on Caribbean islands (Cooke et al. 2016).

The story of platyrrhines seems to be one of amazing sweepstakes dispersal, followed by rapid diversification and widespread geographic colonization of much of South America. After that, dramatic extinctions resulted in the current, much smaller geographic distribution of platyrrhines. These extinctions were probably caused by changing climates, leading to the contraction of forests. Platyrrhines dispersed to the Caribbean and to Central America, with subsequent extinctions in those regions that might have been related to interactions with humans. Unlike anthropoids of the Old World, platyrrhines do not seem to have evolved any primarily terrestrial forms and so have always been highly dependent on forests.

SPECIAL TOPIC: JONATHAN PERRY AND PRIMATES OF THE EXTREME SOUTH

Many primates are very vulnerable to ecological disturbance because they are heavily dependent on fruit to eat and trees to live in. This is one reason why so many primates are endangered today and why many of them went extinct due to climatic and vegetational changes in the past. Jonathan Perry's paleontological research focuses on primates that lived on the edge of their geographic distribution. This research has taken him to two extremes in the Americas: extreme southern Patagonia and the Canadian prairies.

Santa Cruz Province in Argentina is as far south as primates have ever lived. The Santa Cruz fauna of the Miocene has yielded a moderate diversity of platyrrhines, each with slightly different dietary adaptations. These include *Homunculus* (Table 8.1), first described by Florentino Ameghino in 1891 (Figure 8.17). Recent fieldwork by Perry and colleagues in Argentina has revealed several skulls of *Homunculus* as well as many parts of the skeleton (Kay et al. 2012). The emerging profile of this extinct primate is one of a dedicated arboreal quadruped that fed on fruits and leaves. Many of the foods eaten by *Homunculus* must have been very tough and were probably covered and impregnated with grit; we suspect this because the cheek teeth are very worn down, even in young individuals, and because the molar tooth roots were very large, presumably to resist strong bite forces (Perry et al. 2010, 2014).

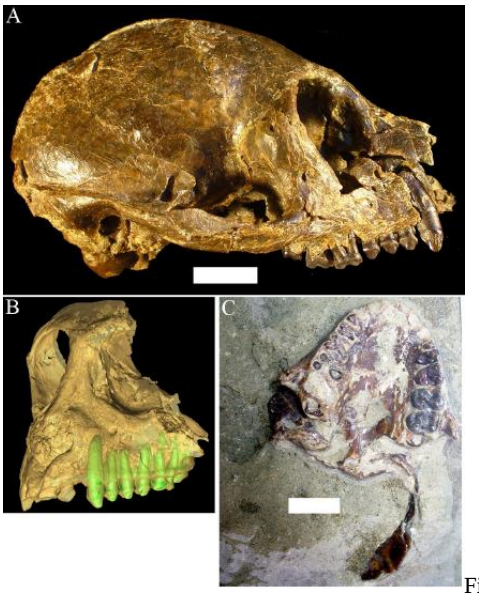


Figure 2.2.4.1: Representative specimens of *Homunculus patagonicus*. A, adult cranium in lateral view. B, adult cranium surface reconstructed from microCT scans, with the teeth segmented out. C, juvenile cranium. White scale bars are 1cm long.

Perry began working in Argentina while a graduate student at Duke University. He participated as a field assistant in a team led by his Ph.D. advisor, Richard F. Kay, and Argentine colleagues Sergio F. Vizcaíno and M. Susana Bargo. Most of the localities examined belong to a suite of beach sites known since the 1800s and visited by many field parties from various museums in the early 1900s. Since 2003, their international team of paleontologists from the U.S. and Argentina has visited these localities every single year (Figure 8.18). Over time, new fossils and new students have led to new projects and new approaches, including the use of microcomputed tomography (microCT) to visualize and analyze internal structures of the skeleton.



Figure 2.2.4.2: Field localities in Argentina and Canada. A, Cañadon Palos locality, coastal Santa Cruz Province, Argentina. B, Swift Current Creek locality, southwest Saskatchewan, Canada.

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2.2.5: Planet of Apes

Geologic Activity and Climate Change in the Miocene

The Miocene Epoch was a time of mammalian diversification and extinction, global climate change, and ecological turnover. In the Miocene, there was an initial warming trend across the globe with the expansion of subtropical forests, followed by widespread cooling and drying with the retreat of tropical forests and replacement with more open woodlands and eventually grasslands. It was also a time of major geologic activity. On one side of the globe, South America experienced the rise of the Andes Mountains. On the other side, the Indian subcontinent collided with mainland Asia, resulting in the rise of the Himalayan Mountains. In Africa, volcanic activity promoted the development of the East African Rift System. Critical to the story of ape evolution was the exposure of an intercontinental landbridge between East Africa and Eurasia, permitting a true planet of apes (Figure 8.19).

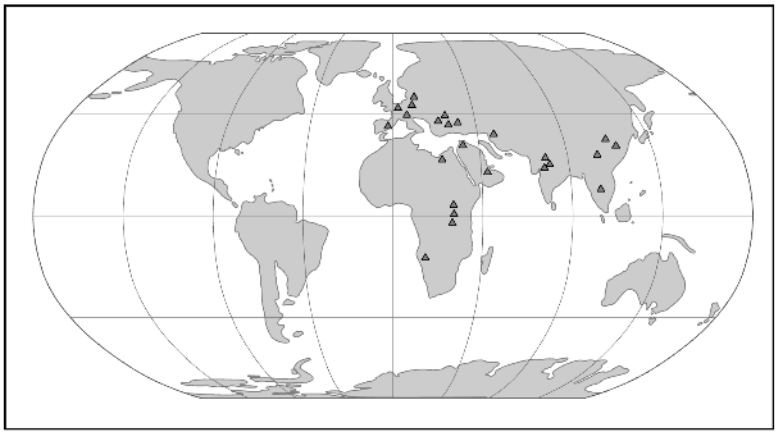


Figure 2.2.5.1: Map of the world in the Miocene, highlighting fossil ape localities.

Geographic Distribution: Africa, Asia, Europe

The world of the Miocene had tremendous ape diversity compared to today. The earliest records of fossil apes are from Early Miocene deposits in Africa. However, something dramatic happened around 16 million years ago. With the closure of the ancient Tethys Sea, the subsequent exposure of the *Gomphotherium* Landbridge, and a period of global warming, the Middle–Late Miocene saw waves of emigration of mammals (including primates) out of Africa and into Eurasia, with evidence of later African re-entry for some (Harrison 2010). Some of the mammals that dispersed from Africa to Eurasia and back were apes. Though most of these early apes left no modern descendants, some of them gave rise to the ancestors of modern apes—including **hominins** (Figure 8.20).

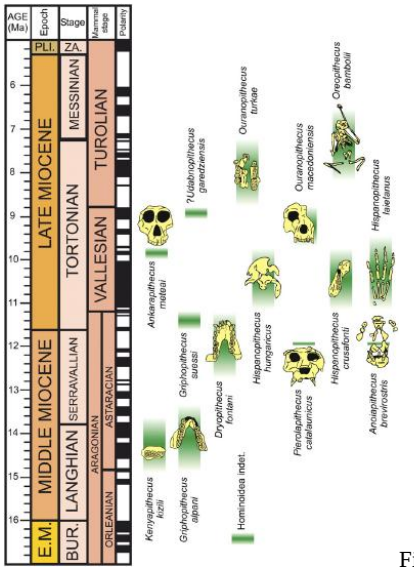


Figure 2.2.5.1: Representative Miocene apes set against a geologic time scale. Casanova-Vilar et al. (2011).

Where Are the Monkeys? Old World Monkey Diversity in the Miocene



Figure 2.2.5.3: Skull of *Victoriapithecus macinnesi* (Musee d'Histoire Naturelle, Paris).

Whereas the Oligocene deposits in the Fayum of Egypt have yielded the earliest-known catarrhine fossils, the Miocene demonstrates some diversification of Cercopithecoidea. However, compared to the numerous and diverse Miocene apes (see below), monkeys of the Miocene are very rare and restricted to a single extinct family, the Victoriapithecidae (Table 8.1). This family contains the earliest definite Old World monkeys. These monkeys are known from northern and eastern Africa between 20 million and 12.5 million years ago (Miller et al. 2009). The best known early Old World monkey is *Victoriapithecus* (Figure 8.21; Table 8.1), a small-bodied (approximately 7 kg; 15 lbs.), small-brained monkey with a long sloping face and round, narrowly spaced orbits. *Victoriapithecus* shares some cranial features with *Aegyptopithecus*; for example, both have a deep malar region of the zygomatic bone and a well-developed sagittal crest (Benefit and McCrossin 1997; Fleagle 2013). Beginning in the Early Miocene, and certainly by the Middle Miocene, bilophodonty, known to be a hallmark of molar teeth of modern Old World monkeys, was present to some extent. Although this dental feature is often indicative of increased leaf-processing efficiency in modern Old World monkeys, *Victoriapithecus* has been reconstructed as being more frugivorous and perhaps spent more time on the ground (terrestrial locomotion) than in the trees (arboreal locomotion; Blue et al. 2006). The two major groups of Old World monkeys today are cercopithecines and colobines. The earliest records demonstrating clear members of each of these two groups are at the end of the Miocene. Examples include the early colobine *Microcolobus* from Kenya and the early cercopithecine *Pliopapio* from Ethiopia.

The Story of Us, the Apes

African Ape Diversity

The Early Miocene of Africa has yielded around 14 genera of early apes (Begun 2003). Many of these taxa have been reconstructed as frugivorous arboreal quadrupeds (Kay 1977).

One of the best studied of these genera is the East African *Proconsul* (Family Proconsulidae; Table 8.1), a short-faced ape with generalized dentition and above-branch locomotor behaviors (Begun 2007). Several species have been described, with body mass reconstructions ranging from 17 to 50 kg (approximately 37–110 lbs.). A paleoenvironmental study reconstructed the habitat of *Proconsul* to be a dense, closed-canopy tropical forest (Michel et al. 2014). One of the most interesting questions about this taxon is whether or not it possessed a tail, a lack of which is an important characteristic for distinguishing living apes from Old World monkeys. No caudal vertebrae (tail bones) have been found in direct association with *Proconsul* postcrania, and the morphology of the sacrum is consistent with *Proconsul* lacking a tail (Russo 2016; Ward et al. 1991).

Overall, the African ape fossil record in the Late Miocene is sparse, with seven fossil localities dating between eleven and five million years ago (Pickford et al. 2009). Nevertheless, most species of great apes live in Africa today. Where did the progenitors of modern African apes arise? Did they evolve in Africa or somewhere else? The paucity of apes in the Late Miocene of Africa stands in contrast to the situation in Eurasia. There, ape diversity was high. Furthermore, several Eurasian ape fossils show morphological affinities with modern hominoids (apes). This has suggested to some paleoanthropologists that the ancestors of modern African great apes recolonized Africa from Eurasia toward the end of the Miocene (Begun 2002). However, discoveries of Late Miocene hominoids like the Kenyan *Nakalipithecus* (9.9 million to 9.8 million years ago) and the Ethiopian *Chororapithecus* (10.7 million to 10.1 million years ago) fuel an alternative hypothesis—namely that African hominoid diversity was maintained throughout the Miocene and that one of these taxa might, in fact, be the last common ancestor of extant African apes (Kunimatsu et al. 2007). The previously underappreciated diversity of Late Miocene apes in Africa might be due to poor sampling of the fossil record in Africa.

Eurasian Ape Diversity

With the establishment of the *Gomphotherium* Landbridge (a result of the closure of the Eastern Mediterranean seaway; Rögl 1999), the Middle Miocene was an exciting time for hominoid radiations outside of Africa (see Figure 8.20). Eurasian hominoid species exploited their environments in many different ways in the Miocene. Food exploitation ranged from soft-fruit feeding in some taxa to hard-object feeding in others, in part owing to seasonal fluctuations and the necessary adoptions of fallback foods (DeMiguel et al. 2014). For example, the molars of *Oreopithecus bambolii* (Family Hominidae) have relatively long lower-molar shearing crests, suggesting that this hominoid was very folivorous (Ungar and Kay 1995). Associated with variation in diet, there is great variation in the degree to which cranial features (e.g., zygomatic bone or supraorbital tori) are developed across the many taxa (Cameron 1997); however, Middle Miocene fossils tend to exhibit relatively thick molar enamel and relatively robust jaws (Andrews and Martin 1991).

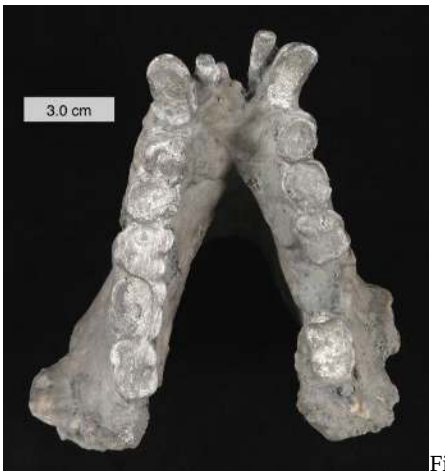


Figure 2.2.5.4: Cast of the mandible of *Gigantopithecus blacki*.

One of the most extreme examples of ape robusticity is the Asian hominoid, *Gigantopithecus* (Table 8.1). Known only from teeth and jaws (e.g., Figure 8.22), this ape probably weighed as much as 270 kg (595 lbs.) and was likely the largest primate ever (Bocherens et al. 2017). Because of unique features of its teeth (including molarized premolars and patterns of wear) and its massive size, it has been reconstructed as a bamboo specialist, somewhat like the modern panda. Small silica particles (phytoliths) from grasses have been found stuck to the molars of *Gigantopithecus* (Ciochon et al. 1990). Recent studies evaluating the carbon

isotope composition of the enamel sampled from *Gigantopithecus* teeth suggest that this ape exploited a wide range of vegetation, including fruits, leaves, roots, and bamboo (Bocherens et al. 2017).

In Spain, the cranium with upper dentition, part of a mandible, and partial skeleton of *Pliobates* (Family Pliobatidae), a small-bodied ape (4–5 kg; 9–11 lbs.), was discovered in deposits dating to 11.6 million years ago (Alba et al. 2015). The authors of the study reconstructed this European catarrhine as a frugivore that overlapped in relative brain size with modern cercopithecoids. The fossilized postcrania of *Pliobates* suggest that this ape might have had a unique style of locomotion, including the tendency to walk across the branches of trees with its palms facing downward and flexible wrists that permitted rotation of the forearm during climbing. However, the anatomy of the distal humerus differs from those of living apes in ways that suggest that *Pliobates* was less efficient at stabilizing its elbow while suspended (Benefit and McCrossin 2015). Two other recently described apes from Spain, *Pierolapithecus* and *Anoiapithecus*, are known from relatively complete skeletons. *Pierolapithecus* had a very projecting face and thick molar enamel as well as some skeletal features that suggest (albeit controversially) a less suspensory locomotor style than in extant apes (Moyà-Solà et al. 2004). In contrast to *Pierolapithecus*, the slightly younger *Anoiapithecus* has a very flat face (Moyà-Solà et al. 2009).



Figure 2.2.5.5: Skeleton of *Oreopithecus bambolii*.

Postcranial evidence for suspensory or well-developed orthograde behaviors in apes does not appear until the Late Miocene of Europe. Primary evidence supporting these specialized locomotor modes includes the relatively short lumbar vertebrae of *Oreopithecus* (Figure 8.23) and *Dryopithecus* (Maclatchy 2004). The Late Miocene saw the extinction of most of the Eurasian hominoids in an event referred to as the Vallesian Crisis (Agustí et al. 2003). Among the latest surviving hominoid taxa in Eurasia were *Oreopithecus* and *Gigantopithecus*, the latter of which held out until the Pleistocene in Asia and was probably even sympatric with *Homo erectus* (Cachel 2015).

The Origins of Extant Apes

The fossil record of the extant apes is somewhat underwhelming: it ranges from being practically nonexistent for some taxa (e.g., chimpanzees) to being a little better for others (e.g., humans). There are many possible reasons for these differences in fossil abundance, and many are associated with the environmental conditions necessary for the fossilization of bones. One way to understand the evolution of extant apes that is not so dependent on the fossil record is via molecular evolutionary analyses. This can include counting up the differences in the genetic sequence between two closely related species to estimate the amount of time since these species shared a common ancestor. This is called a molecular clock, and it is often calibrated using fossils of known absolute age that stand in for the last common ancestor of a particular clade. Molecular clock estimates have placed the split between Hylobatidae and Hominidae between 19.7 million and 24.1 million years ago, followed by an African ape and Asian ape split between 15.7 million and 19.3 million years ago, and, finally, with the more recent radiation of Hylobatidae into its current genera between 6.4 million and 8 million years ago (Israfil et al. 2011).

Lesser Ape Origins and Fossils

Unfortunately, the fossil record for the lesser apes is meager, particularly in Miocene deposits. One possible early hylobatid is *Laccopithecus robustus*, a Late Miocene catarrhine from China (Harrison 2016). Although it does share some characteristics with modern gibbons and siamangs (including an overall small body size and a short face), *Laccopithecus* most likely represents a primitive stem catarrhine and is therefore distantly related to extant apes (Jablonski and Chaplin 2009). A more likely candidate for the hylobatid stem is another Late Miocene taxon from China, *Yuanmoupithecus xiaoyuan* (Table 8.1). Interpretation of its phylogenetic standing, however, is complicated by contradicting dental features—some of them quite primitive—which some believe best place *Yuanmoupithecus* as a stem hylobatid (Harrison 2016). The history of Hylobatidae becomes clearer in the Pleistocene, with fossils representing extant genera.

Great Ape Origins and Fossils

The most extensive fossil record of a modern great ape is that of our own genus, *Homo*. The evolution of our own species will be covered in the next chapter. The evolutionary history of the Asian great ape, the orangutan (*Pongo*), is becoming clearer. Today, orangutans are found only on the islands of Borneo and Sumatra. However, Pleistocene-aged teeth, attributed to *Pongo*, have been found in Cambodia, China, Laos, Peninsular Malaysia, and Vietnam—demonstrating the vastness of the orangutan's previous range (Ibrahim et al. 2013; Wang et al. 2014). *Sivapithecus* from the Miocene of India and Pakistan is represented by many specimens, including parts of the face. *Sivapithecus* is very similar to *Pongo*, especially in the face, and it probably is closely related to ancestral orangutans (Pilbeam 1982). Originally, jaws and teeth belonging to the former genus *Ramapithecus* were thought to be important in the origin of humans (Simons 1961), but now these are recognized as specimens of *Sivapithecus* (Kelley 2002). Postcranial bones of *Sivapithecus*, however, suggest a more generalized locomotor mode—including terrestrial locomotion—than seen in *Pongo* (Pilbeam et al. 1990).

In Africa, the first fossil to be confidently attributed to *Pan*, and known to be the earliest evidence of a chimpanzee, was described based on teeth found in Middle Pleistocene deposits in the Eastern Rift Valley of Kenya (McBrearty and Jablonski 2005). Paleoenvironmental reconstructions of this locality suggest that this early chimpanzee was living in close proximity to early *Homo* in a closed-canopy wooded habitat. Similarly, fossil teeth and mandibular remains attributed to two species of Middle-Late Miocene apes—*Chororapithecus abyssinicus* (from Ethiopia; Suwa et al. 2007) and *Nakalipithecus nakayamai* (from Kenya; Kunimatsu et al. 2007)—have been suggested as basal members of the gorilla clade.

Clearly, more work is needed to fill in the large gaps in the fossil record of the nonhuman great apes. The 20th century witnessed the discovery of many hominin fossils in East Africa, which have been critical for improving our understanding of human evolution. While 21st-century conservationists fight to prevent the extinction of the living great apes, perhaps efforts by 21st-century paleoanthropologists will yield the evolutionary story of these, our closest relatives.

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2.2.6: Key Terms

Key Terms

Adapoidea: Order: Primates. One of the earliest groups of euprimates (true primates; earliest records from the early Eocene).

Anthropoids: Group containing monkeys and apes, including humans.

Auditory bulla: The rounded bony floor of the middle ear cavity.

Bilophodonty: Dental condition in which the cusps of molar teeth form ridges (or lophs) separated from each other by valleys (seen, e.g., in modern Old World monkeys).

Catarrhines: Order: Primates; Suborder: Anthropoidea; Infraorder: Catarrhini. Group containing Old World monkeys and apes, including humans.

Clade: Group containing all of the descendants of a single ancestor. A portion of a phylogenetic tree represented as a bifurcation (node) in a lineage and all of the branches leading forward in time from that bifurcation.

Convergent evolution: The independent evolution of a morphological feature in animals not closely related (e.g., wings in birds and bats).

Crown group: Smallest monophyletic group (clade) containing a specified set of extant taxa and all descendants of their last common ancestor.

Diagnosis: The features that allow you to recognize a group.

Diastema: Space between adjacent teeth.

Diffuse coevolution: The ecological interaction between whole groups of species (e.g., primates) with whole groups of other species (e.g., fruiting trees).

Ectotympanic: Bony ring or tube that holds the tympanic membrane (eardrum).

Euprimates: Order: Primates. True primates or primates of modern aspect.

Haplorhines: Group containing catarrhines, platyrrhines, and tarsiers.

Hominins: Modern humans and any extinct relatives more closely related to us than to chimpanzees.

Mandibular symphysis: Fibrocartilaginous joint between the left and right mandibular segments, located in the midline of the body.

Old World: Africa and Eurasia.

Omomyoidea: Order: Primates; Superfamily: Omomyoidea. One of the earliest groups of euprimates (true primates; earliest record in the early Eocene).

Petrosal bone: Petrous portion of the temporal bone. It houses the inner ear apparatus, among other things.

Plagiaulacoid: Dental condition where at least one of the lower cheek-teeth (molars or premolars) is a laterally compressed blade.

Platyrrhines: Order: Primates; Suborder: Anthropoidea; Infraorder: Platyrrhini. Group containing New World monkeys.

Plesiadapiforms: Order: Plesiadapiformes. Archaic primates or primate-like placental mammals (Early Paleocene–Late Eocene).

Stem: Taxa are basal to a given crown group but are more closely related to the crown group than to the closest living sister taxon of the crown group.

Strepsirrhines: Order: Primates; Suborder: Stresirrhini. Group containing lemurs, lorises, and galagos (does not include tarsiers).

Toothcomb: Dental condition found in modern strepsirrhines in which the lower incisors and canines are laterally compressed and protrude forward at a nearly horizontal inclination. This structure is used in grooming.

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CHAPTER OVERVIEW

3: Conservation

3.1: Primate Conversation

3.1.1: Current Conservation of Nonhuman Primates

3.1.2: Threats to Primates

3.1.3: What Can Be Done?

3.1.4: Future Perspectives

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SECTION OVERVIEW

3.1: Primate Conversation

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Learning Objectives

- Understand the current conservation status of the world's primates and the criteria that researchers and conservationists use to make these assessments.
- Recognize the many threats that negatively impact primate survival.
- Understand how these threats uniquely affect primates because of characteristics like slow growth rates, long interbirth intervals, strong social bonds, and cultural behavior.
- Become aware of the many ways in which primates are significant to ecological processes, our understanding of human evolution, human cultures, and local economies.
- Learn about ways that people, wherever they may live, can work to protect primates.

We are field primatologists interested in understanding primates in their natural environments and in contributing to their conservation. Our research focuses on a diversity of primate species that occur in a wide range of habitats throughout the tropics; however, these species and their habitats are subject to many similar threats. As human populations continue to grow (Figure B.1), primates are being pushed out of their natural home ranges and are being forced to occupy increasingly smaller and more isolated patches of land. Humans and primates are sharing more spaces with one another, making it easier for primates to be hunted or captured and for diseases to spread from humans to primates (and vice versa). Even when primates are not directly threatened by human activities, human-induced climate change is altering local ecosystems at an alarming rate. Local political instability exacerbates all of these problems. Our research causes us to think about these issues on a daily basis. Understanding how these threats affect the primates we study is a very important part of what we do. Ultimately, the research of field primatologists like us is important for documenting the status of wild primate populations, as well as for understanding how they respond to these threats and for gaining insights into the kinds of efforts that can help to improve their chances of survival in an uncertain future.

This appendix begins with a review of the current status of primates and the criteria used in these assessments. We then describe the major threats to primates, explain why primates are important, and consider what can be done to improve their chances. We conclude with a brief consideration of the future for primates.

Figure B.1 World population growth by region. Global populations are projected to exceed 11 billion people by 2100 (UN Population Division 2017).

3.1.1: Current Conservation of Nonhuman Primates

3.1.2: Threats to Primates

3.1.3: What Can Be Done?

3.1.4: Future Perspectives

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3.1.1: Current Conservation of Nonhuman Primates

Diversity of Primates

The order Primates is one of the most diverse groups of mammals on the planet, with 504 species in 79 different genera currently recognized (Figure B.2; Estrada et al. 2017). Recently new genera, species, and subspecies of nonhuman primates (henceforth, simply “primates”) have been recognized, in some cases as a result of new discoveries and new data, but also because of revisions to taxonomic classification systems based on different species concepts (Groves 2014; Lynch Alfaro et al. 2012; Rylands and Mittermeier 2014).

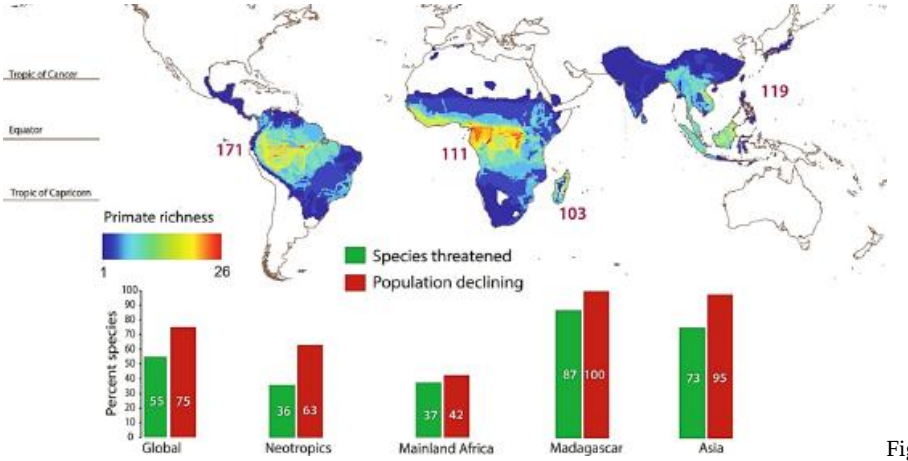


Figure 3.1.1.1: The global distribution and species richness of primates and the percentage of those threatened with extinction and declining populations. The numbers next to each geographic area indicate the current species present in that location. The bars below show the percentage of species threatened with extinction (in green) and the percentage of species with declining populations in each region (in red).



Figure 3.1.1.2: Mountain gorilla (Gorilla beringei beringei) in Bwindi Impenetrable National Park, Uganda. Mountain gorillas are classified as endangered and are only found in the Virungas area of Rwanda and the Democratic Republic of Congo and the Bwindi forest of Uganda (Hickey et al. 2018; Kalpers et al. 2003). This species has suffered tremendously due to habitat destruction, poaching, political unrest, and war (Kalpers et al. 2003).



Figure 3.1.1.3: A female northern muriqui (Brachyteles hypoxanthus) with infant at the Feliciano Miguel Abdala Private Natural Heritage Reserve outside of Caratinga, Brazil. Muriquis are found exclusively in the Atlantic Forest of southeastern Brazil. The destruction and fragmentation of these forests have caused this species to be listed as Critically Endangered (Strier et al. 2017). Although still threatened, the continued efforts of the Muriqui Project of Caratinga have brought this species back from the brink of extinction.

Wild primates occur in 90 countries around the world, but two-thirds of all species are found in only four countries: Brazil, Madagascar, Democratic Republic of Congo, and Indonesia (Estrada et al. 2017; Estrada et al. 2018). An estimated 60% of primate species are threatened with extinction and 75% are experiencing population declines (Estrada et al. 2017, see Figure B.2). Yet despite these discouraging statistics, there are a growing number of populations recovering as a result of research and conservation efforts. For example, the population of mountain gorillas (Figure B.3) initially studied by Dian Fossey in Rwanda in 1967 has increased from 250 gorillas in 1981 to 339 in 2008 as a result of ongoing research and conservation efforts that include highly controlled ecotourism (Robbins et al. 2011). Similarly, one population of northern muriqui monkeys (Figure B.4) inhabiting a small privately owned forest fragment in southeastern Brazil's Atlantic Forest increased from about 50 individuals to nearly 350 individuals as a result of increased habitat protection over the course of the Muriqui Project of Caratinga, a long-term field study initiated more than 35 years ago by one of the authors of this appendix (Strier and Mendes 2012).

International Union for the Conservation of Nature (IUCN)

In conservation, it is crucial to have a global standard to assess and recognize the conservation status of species. The International Union for the Conservation of Nature (IUCN) formed the Red List for Threatened Species in 1994 to determine species extinction risks (IUCN 2017). Scientists submit assessments of species to the IUCN, which are subsequently categorized based on the size and distribution of species' numbers and available habitat. The categories range from "data deficient," when not enough is known, to "least concern," "near threatened," "vulnerable," "endangered," "critically endangered," "extinct in the wild," and "extinct." Threatened species are classified as "vulnerable," "endangered," or "critically endangered," with the most critically endangered species being those whose numbers are fewer than 250 mature individuals and continuing to decline or whose habitats are severely fragmented (Figure B.5; IUCN 2017).

Table 18.1.1: International Union for Conservation of Nature (IUCN) Criteria for Threatened Taxa. Updated from Strier 2011a. Source: Simplified and condensed from IUCN Species Survival Commission, 2012.

Critically Endangered (CR): Facing an extremely high risk of extinction in the wild due to any of the following:
A. Reduction in population size of 80%–90% over the last ten years or three generations, depending on the causes and reversibility of the reductions;
B. Extent of occurrence <100 km2 or area of occupancy <10 km2 or both;
C. Population size estimated to number fewer than 250 mature individuals and to be declining or unevenly distributed;
D. Population size estimated to number fewer than 50 mature individuals;
E. Probability of extinction within ten years or three generations is at least 50%.
Endangered (EN): Facing a very high risk of extinction in the wild due to any of the following:
A. Reduction in population size of 50%–70% over the last ten years or three generations, depending on the causes and reversibility of the reductions;
B. Extent of occurrence <5000 km2 or area of occupancy <500 km2 or both;
C. Population size estimated to number fewer than 2,500 mature individuals and to be declining or unevenly distributed;
D. Population size estimated to number fewer than 250 mature individuals;
E. Probability of extinction within 20 years or five generations is at least 20%.
Vulnerable (VU): Facing a high risk of extinction in the wild due to any of the following:
A. Reduction in population size of 30%–50% over the last ten years or three generations, depending on the causes and reversibility of the reductions;
B. Extent of occurrence <20,000 km2 or area of occupancy <2000 km2 or both;
C. Population size estimated to number fewer than 10,000 mature individuals and to be declining or unevenly distributed;
D. Population size estimated to number fewer than 1,000 mature individuals;
E. Probability of extinction within 100 years is at least 10%.

The IUCN has a committee specifically dedicated to primates, the IUCN Species Survival Commission (SSC) Primate Specialist Group. This group collaborates with the International Primatological Society (IPS), Conservation International (CI), and the Bristol Zoological Society (BZS) every two years to publish “Primates in Peril: The World’s 25 Most Endangered Primates.” These lists are created at IPS open meetings and are intended to focus attention on all endangered primates by highlighting the plights of some of the most critically endangered (Schwitzer et al. 2017).

Identifying Priorities in Primate Conservation

It is important to consider extinction risk in making conservation decisions, thus the IUCN Red list and the “Primates in Peril” reports are factors in deciding how to allocate resources and funding. Some primate species are found only in biodiversity hot spots, or areas that contain high levels of species diversity and include primates that are endemic to the area and genetically unique (Sechrest et al. 2002). Hot spots are often considered conservation priorities because protecting these areas can result in the protection of large numbers of species. In addition, some conservation organizations focus on highly charismatic primate species (e.g., primates that are large, closely related to humans, or well-known from zoos, such as the golden lion tamarin) to garner attention and resources for conservation (Figure B.6). However, dramatic declines of charismatic species indicate that charisma is not enough (Estrada et al. 2017). For example, it is estimated that the population of Bornean orangutans (*Pongo pygmaeus*) decreased by 100,000 individuals between 1999 and 2015, despite being very popular with the general public (Voigt et al. 2018). In making conservation decisions, primatologists may also consider the importance of genetically unique primates, such as the aye-aye (*Daubentonia madagascariensis*), the last remaining species within its genus in order to preserve evolutionary history (Strier 2011a).

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3.1.2: Threats to Primates

Hunting, Poaching, and Wildlife Trade



Figure 3.1.2.1: A male Bornean orangutan (Pongo pygmaeus). This species' large size and close genetic relatedness to humans often make them appealing to the public, categorizing them as a "charismatic species." Such charismatic animals may garner more resources for conservation. In species like the Critically Endangered Bornean orangutan, whose habitat is highly threatened, this attention can be crucial to their survival (Ancrenaz et al. 2016).

Hunting represents one of the most critical threats to primates (Figure B.7). Bushmeat, which is the meat of wild animals, has historically been a staple diet in many societies. However, human population growth and economic development have increased the commercialization of bushmeat hunting, thereby increasing its impact (Estrada et al. 2017). The increased availability and use of shotguns has also dramatically increased the volume of carcasses that hunters capture (Cronin et al. 2015). Across 89 markets in Nigeria and Cameroon, John Fa and colleagues (2015) calculated that almost 150,000 primate carcasses (from at least 16 different species) were sold annually. In one market on the Liberia/Ivory Coast border, Ryan Covey and Scott McGraw (2014) estimated that the carcasses of nearly 9,500 primates (from at least nine different species) were sold per year, resulting in an almost 3% annual reduction in the local primate population.

Not all primates are hunted specifically for food. Biomedical researchers use primates as models for understanding human biology and as test subjects for the development of vaccines, drugs, and hormones (Conaway 2011). Many of these experiments require large numbers of primates; therefore biomedical facilities often require a continuous supply of primates. To support the international demand for biomedical research test subjects, rhesus macaques (*Macaca mulatta*) in northern and central India experienced a 90% decline in populations over a 28-year period, from 1959 to 1986 (Southwick and Siddiqi 1988). Between 2007 and 2008, a single biomedical laboratory purchased roughly 4,000 nocturnal monkeys for over 100,000 USD through a network of 43 traders across Brazil, Colombia, and Peru (Maldonado et al. 2009).



Figure 3.1.2.2: A female gelada (Theropithecus gelada) with a snare around its neck in central Ethiopia. Many rural hunters prefer to hunt using snare traps, which can be easily constructed and offer a more affordable and accessible alternative to firearms (Noss 1998; Tumusiime et al. 2010). Snare traps are constructed out of wire nooses anchored to trees or the ground. Snares are designed to tighten around prey as they struggle to free themselves. Though larger primates are sometimes able to detach snares from their anchored positions, the snare often remains wrapped around the affected body part and can result in loss of circulation, infection, and mutilation (Yersin et al. 2017).

Aside from biomedical research, captured primates are both legally and illegally sold to pet owners, zoos, tourist centers, and circuses. In Peru, it is estimated that, as recently as 2015, hundreds of thousands of primates are illegally traded every year, comparable to levels of trade prior to a 1973 national ban on primate exportation (Shanee et al. 2017). Once captured, primates may spend over a week in transit from a rural village to a coastal market. To make the transportation of primates more manageable, common trafficking strategies include sedation, asphyxiation, electrocution, and the removal of teeth. As these conditions severely affect the health of the trafficked primates, many perish during the journey while others die within the hands of authorities. Out of the 77 greater slow lorises (*Nycticebus coucang*) confiscated from a single wildlife trader in Indonesia, 22 died from either trauma or from the severity of their wounds (Fuller et al. 2018). Even when primates are successfully confiscated from wildlife traders, it is not uncommon for authorities to either resell or gift these animals to friends and family (Shanee et al. 2017).

To help curb illegal trafficking of animals, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) was established in 1973 and ratified in 1975. Under this treaty, the 183 participating countries work together to both regulate the international trade of wildlife and to prevent the overexploitation of wild populations. While only some primates are listed as endangered or threatened under the Endangered Species Act (ESA), all primates are listed under CITES. According to the CITES database, more than 450,000 live primates were traded over the past 15 years (CITES n.d.). However, as the CITES database only includes information formally reported by each country, the real number of primates involved is likely to be much higher.

Habitat Loss, Fragmentation, and Degradation

The geographic distribution of many primate species has been severely limited by habitat loss. A recent analysis showed human demands for agricultural land threaten 76% of primate species, followed by demands for logging (60%) and livestock farming (31%) (Estrada et al. 2017). Habitat loss is not new and has affected the distribution of some primate species for thousands of years. Since the Bronze Age, for example, increases in human land use throughout China have been associated with corresponding decreases in suitable habitats for golden snub-nosed monkeys (*Rhinopithecus roxellana*) (Wang et al. 2014). However, our ever-growing need for food, water, and other natural resources has drastically decreased primate habitats globally (Figure B.8). From 2000 to 2013, roughly 220,000 km2 of tropical forest have been completely deforested in the Brazilian Amazon alone (Tyukavina et al. 2017). Since the start of oil palm development in Indonesia's Ketapang District in 1994, over 65% of habitats without government protection have been allocated to the oil palm industry (Carlson et al. 2012). Even within protected areas, primate habitats are rapidly declining. In South Asia, 36% of surveyed protected areas had more than half of their habitat modified for human use, many of which experienced near-total habitat transformation (Clark et al. 2013). One of these protected areas, the Borajan Reserve Forest in India, saw a more than two-thirds reduction in suitable habitat within a three-year period, resulting in severe population declines for five primate species (Srivastava et al. 2001).



Figure 3.1.2.3 Cattle graze in a newly formed papaya plantation, which was once forested land in Montagne des Français, Madagascar. Forests are cleared throughout the tropics for both large-scale commercial agricultural as well as for subsistence farming. Conversion for agricultural expansion alone accounts for nearly 75% of all tropical deforestation (Hosonuma et al. 2012). While some primates may still be able to utilize these agricultural matrix environments for foraging and resting, it may put them in danger because of potential heightened human-wildlife conflict.

Habitat fragmentation compounds the effects of habitat loss. Whereas habitat loss reduces the total area in which primates can survive, habitat fragmentation divides large, contiguous primate habitats into smaller isolated patches (Figure B.9). The construction of road networks cutting through savannas, forests, and other primate habitats is a key driver of this fragmentation.

Within the next half-century, over 25,000,000 kmof new roads are expected to be built, many of which in developing nations through primate habitats (Laurance et al. 2014). By fragmenting habitats, it becomes increasingly challenging for primates (particularly arboreal primates) to disperse between isolated habitat patches. While only 0.1% of black-and-white snub-nosed monkey (*Rhinopithecus bieti*) habitat was lost to the construction of China National Highway 214, movement between habitat patches on either side of the highway was reduced by over 20% (Clauzel et al. 2015). In the long run, habitat fragmentation can force primate populations into genetic bottlenecks, which occur when populations become so small that genetic diversity in them is severely reduced. In the forest fragments of Manaus, Brazil, groups of pied tamarins (*Sanguinus bicolor*) that historically formed one biological population were found to harbor only a subset of the genetic diversity previously exhibited in the region (Farias et al. 2015). Furthermore, primates living in fragments with scarce resources experience elevated levels of stress, which can also have long-term consequences on the health of individuals and populations (Rimbach et al. 2014).

Figure Runaway argument for \eatSpaces? Forest cleared for cattle ranching in the province of Manabí, Ecuador. Cattle ranching is currently the main driver of deforestation in South American countries (Steinweg et al. 2016). Landholders clear and burn primary forests to convert them into cattle pastures, and when yield begins to decline, they typically move to another old-growth forest and the cycle begins again. Not surprisingly, tropical forests are disappearing faster than any other biome (Aide et al. 2013; Wright 2005). Halting deforestation through community-based conservation programs is one of the main objectives of many non-governmental organizations, such as Proyecto Washu in Ecuador.

Figure Runaway argument for \eatSpaces? An industrial-sized truck leaves the Montagne des Français region in Madagascar, with dozens of bags of charcoal in tow to be delivered to a nearby town. Much of sub-Saharan Africa still relies on charcoal and other fuelwoods as a main source of energy for cooking and heating. Fuelwood collection and charcoal production are the main proximate drivers of forest degradation throughout Africa (Hosonuma et al. 2012). Degradation and forest loss can lead to a suite of harmful effects for primates living in these regions.

Aside from habitat loss, other drivers of habitat degradation may affect primate populations. For example, streams can carry toxic chemicals used for agriculture into local habitats where they are either directly or indirectly consumed by primates. In Uganda, chimpanzees (*Pan troglodytes*) living within the Sebitoli Forest have been spotted with facial and limb deformities that are suspected of being related to their exposure to pesticides and herbicides used by local tea farmers (Krief et al. 2017). Additionally, invasive species that outcompete native species and alter habitats can affect primate behaviors. In Madagascar, southern bamboo lemurs (*Hapalemur meridionalis*) spent less time feeding in forests dominated by invasive Melaleuca trees (*Melaleuca quinquenervia*) than in forests without these trees (Eppley et al. 2015). Lastly, the use of fuelwood and charcoal is still widely used throughout sub-Saharan Africa as a means to produce heat and energy for cooking (Figure B.10).

Climate Change

Current State

Climate change is one of the most devastating threats facing primates because it compounds preexisting threats, such as habitat degradation and fragmentation. In a little over a century, the earth has seen temperatures rise by 0.85ºC globally, with each decade being warmer than the last (IPCC Climate Change 2014). The resulting changes that occur, many of which are just beginning to be documented, can be unpredictable and cause a range of consequences for biodiversity. Increasingly frequent regional droughts, especially in the Southern Hemisphere, not only affect resource abundance but also create a cascade of other ecosystem disturbances that contribute to increased carbon dioxide production (Zhao and Running 2010). In Kibale National Park, Uganda, Jessica Rothman and colleagues (2015) found that the increasing carbon dioxide levels associated with climate change decreased the nutritional value of leaves, an important food resource for many primates.

Climate change is associated with volatile and unpredictable weather patterns. El Niño Southern Oscillation events (ENSO) influence weather patterns across the globe. Although ENSO events have been occurring for thousands of years, climate change is causing them to occur more frequently and with greater intensity (Wiederholt and Post 2010). The warm air and unpredictable rains that come with an ENSO event can negatively affect food resource abundance. Primates whose diets include high quantities of fruit experience the effects of fruit shortages most strongly (Campos et al. 2015). Madagascar, a primate hot spot and country with high levels of anthropogenic disturbance, is a prime example of how the increased intensity and frequency of climatic events such as ENSO can have consequences for primates (Figure B.11). Amy Dunham and colleagues (2008) found that even the folivorous Milne-Edwards' sifaka (*Propithecus edwarsi*), found within Ranomafana National Park in southeastern Madagascar, would experience severely reduced populations within three generations if ENSO events continued at the current frequency.

Figure Runaway argument for \eatSpaces? An old-growth tree is uprooted after Cyclone Enawo made landfall in northeast Madagascar in March 2017. Ocean surface temperatures are increasing as a result of anthropogenic climate change, which may cause stronger tropical storms. These storms often result in dramatic alterations to ecosystems, changing vegetation composition by damaging trunks and branches of trees (Dinsmore et al. 2018). These changes in habitat structure can in turn have repercussions for primates living in these regions, driving them to alter feeding, moving, and reproductive patterns.

Rapidly changing climate also causes other extreme weather events in primate areas. Due to climate change, hurricanes and cyclones are occurring more frequently. Several studies have looked at the effects on primate populations before and after hurricanes (e.g., Ratsimbazafy 2006; Schaffner et al. 2012; Zimmerman and Kovich 2007). A population of howler monkeys in Belize (*Alouatta pigra*) experienced population reduction and reduced reproduction after a hurricane hit. This response lasted more than three years (Behie and Pavelka 2005; Pavelka and Chapman 2006). However, not all primates are as vulnerable to the effects of major storms. In Kirindy Mitea National Park in western Madagascar, Verreaux's sifakas (*Propithecus verreauxi*) did not suffer reduced population or reproduction, despite a reduction in their food supply following a cyclone (Lewis and Rakontondranaivo 2011). The different responses of these species to catastrophic events is likely related to differences in their behavioral flexibility, such as adjusting the types of foods consumed and the amount of time spent resting, feeding, moving, and socializing by each species (Strier 2017) and evolutionary adaptability (Wright 1999).

Large-Scale Change

On a large scale, the deleterious effects of climate change can make primates' current environments inhospitable. Most primates are adapted to live in tropical environments and many have specialized diets. Climate change alters the flowering and fruiting seasons of many plants, requiring a great deal of dietary flexibility from the organisms that rely on their production (Anderson et al. 2012). Many primates are not capable of this adjustment and would need to shift their habitat range to cope. Unfortunately, habitat loss and fragmentation make these range shifts impossible for many species without human assistance in the form of translocations. Primates have relatively slow life-histories, often producing only one offspring at a time, and their extended juvenile period results in slow evolutionary adaptation to change (Campos et al. 2017). To cope with the large-scale effects of climate change, primates must rely on behavioral flexibility and aid from humans. Primates are projected to have some of the most restricted ranges due to climate change (Schloss et al. 2012), forcing them to utilize a variety of possible, non-preferred habitats

Small-Scale Change

On a small or local scale, the effects of climate change are more fine-tuned and can differ depending on the species. For example, spider monkeys (*Ateles geoffroyi yucatanensis*) exhibited behavioral plasticity after two hurricanes hit Mexico, spending more time resting, feeding on leaves, and in smaller subgroups than they did before the hurricanes (Schaffner et al. 2012). Critically endangered species, such as the northern sportive lemur (*Lepilemur septentrionalis*), are more vulnerable to catastrophic weather events because in small populations the loss of just a few individuals can have major impacts (Figure B.12) (Dinsmore et al. 2016). Species that are not threatened or that have large, intact ranges are not likely to be greatly affected by localized climatic conditions, but they may nonetheless experience local devastation and even extinction (Strier 2017).

Figure Runaway argument for \eatSpaces? A northern sportive lemur (Lepilemur septentrionalis) rests in a tree at Montagne des Français, Madagascar. A Critically Endangered species, the nocturnal northern sportive lemur is estimated to have a population of only ~50 individuals that are restricted to one forest fragment in northern Madagascar. For small populations like the northern sportive lemur, the impacts of climate change can be exacerbated. However, non-governmental organizations, such as Madagascar Biodiversity Partnership (MBP), work with species like the northern sportive lemur to increase their populations and minimize such impacts. MBP has been working at Montagne des Français to monitor northern sportive lemurs and initiate reforestation efforts since 2012.

Disease

Disease is especially intertwined with climate change and has increasingly become a critical threat to primates (Nunn and Altizer 2006). Shifting temperatures, unpredictable precipitation, crowding in fragmented habitats, and increased human contact can contribute to increased disease transmission among primates (Nunn and Gillespie 2016). Mosquito populations, which are vectors of diseases that affect humans and nonhuman primates like Zika virus, yellow fever, and malaria, often thrive in this type of environment and have expanded in recent years (Lafferty 2009). Disease outbreaks have the potential to severely reduce primate populations. In 2016 and 2017, a large yellow fever outbreak devastated several populations of the brown howler monkey (*Alouatta guariba*) endemic to the Atlantic forest of Brazil (Fernandes et al. 2017). Ebola outbreaks have similarly diminished populations of African apes; in 2003 and 2004, an outbreak killed up to 5,000 endangered western gorillas (*Gorilla gorilla*) (Bermejo et al. 2006) and severely reduced populations of chimpanzees (*Pan troglodytes*) (Leroy et al. 2004) in Gabon and the Republic of Congo.

Human encroachment into primate habitats as a result of agricultural expansion, resource extraction, or even through irresponsible eco-tourism or research practices can introduce novel pathogens into both human and nonhuman primate populations (Strier 2017). Due to our close shared lineage, many diseases are communicable between humans and primates, such as Ebola, HIV, tuberculosis, herpes, and other common ailments. Close contact and primate handling are often the most direct ways in which these diseases are transmitted. However, poor hygiene practices, improper waste disposal, and primate provisioning contribute to disease susceptibility in primates (Wallis and Lee 1999). For example, two groups of olive baboons (*Papio cynocephalus anubis*) living in the Masai Mara Game Reserve in Kenya contracted tuberculosis from foraging at contaminated garbage dumps near the tourist lodge (Tarara et al. 1985). Similarly, in Gombe National Park, Tanzania, there is evidence that contact with humans and their domesticated animals in nearby villages caused an outbreak of polio in chimpanzees (*Pan troglodytes*) (Williams et al. 2008). Transmission of diseases through increased human contact can have devastating effects on primate populations that have not built any resistance (Laurance 2015).

Extinction Vortex

Figure Runaway argument for \eatSpaces? A model of the extinction vortex. The extinction vortex shows the threats and pressures that work simultaneously to threaten populations. These pressures are often exacerbated by the compounding effects they have on each other. Once a population has entered the vortex, this cascade of events can prevent recovery, resulting in extinction.

The many threats facing primates that we have listed here are completely interrelated. As such, they tend to interact with one another, creating what is known as an extinction vortex (Figure B.13; Gilpin and Soulé 1986). Habitat fragmentation and loss, hunting, climate change, and disease compound to reduce primate populations at a greater rate than when acting alone. Small populations living in isolated fragments of habitat are disconnected from the rest of their species and are therefore more vulnerable to inbreeding effects. Daniel Brito and colleagues (2008) found that many populations of the critically endangered northern muriqui (*Brachyteles hypoxanthus*) residing in the remaining fragments of the Atlantic Forest would experience genetic decay with possibility of extinction over the next 50 generations if management practices were not put into place. Slow life histories resulting in long interbirth intervals push many species of primates farther into the extinction vortex. Shifting demographics can have dire consequences for primates, thrusting them into a cycle that is hard to break once entered. With the continued presence of threats, many species have a difficult time recovering (Brook et al. 2008; Strier 2011a).

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3.1.3: What Can Be Done?

Role of Research

Systematic and long-term research studies provide some of the most foundational and necessary information for the conservation of endangered primates (Kappeler and Watts 2012). Research provides critical data on essential and preferred feeding resources, life history parameters and reproduction rates, territoriality, the carrying capacity of habitats, and solitary or group social dynamics. Within the last few decades, researchers have also begun to stress the acute need for studies investigating how various primates are responding to human disturbances; how climate change is affecting the behavior, range, and habitat of these species; and the significance of primate biodiversity hotspots (Brown and Yoder 2015; Chapman and Peres 2001; Estrada et al. 2018). Understanding these aspects will provide crucial information for practitioners to make the most effective and species-specific conservation decisions.

Long-term studies on primate species provide some of the most conclusive information on changes occurring to populations in the face of anthropogenic disturbances and climate change. They also provide a suite of direct and indirect conservation contributions to endangered species, and the continual monitoring of populations can deter deleterious anthropogenic actions, allowing for population growth and forest regeneration. For example, the Northern Muriqui Project of Caratinga in Minas Gerais, Brazil, has documented growth of both the muriqui population and the regeneration of the forest via secondary succession (Strier 2010). The project has also invested in future research and conservation by training more than 65 Brazilian students, as well as providing stable jobs for local people, stimulating the local community, and alleviating reliance on forest products for income and survival (Strier 2010; Strier and Boubli 2006; Strier and Mendes 2012). Several other long-term primate studies all over the world have seen similar positive impacts and conservation successes including work in Beza Mahafaly Special Reserve, Berenty Reserve, and Ranomafana National Park, Madagascar; Lomas Barbudal and Santa Rosa National Park, Costa Rica; Khau Yai National Park, Thailand; Amboseli National Park, Kenya; Gombe Stream National Park, Tanzania; Kibale National Park, Uganda, among many others (Kappeler and Watts 2012).

The implementation of novel research techniques can also aid in the conservation of primates and their ecosystems. The use of high-resolution camera traps have become widespread and invaluable in their ability to aid primatologists and conservationists in surveying rare populations, establishing population counts, and assessing behavior (Pebsworth and LaFleur 2014). Camera traps also have the potential to aid in ethical considerations, photographing illegal activities such as poaching. Research is also imperative for making important decisions regarding translocations and reintroductions of animals. Without knowledge of the species' social ecology, demography, and unique learned behaviors—also known as primate traditions or cultures—successful translocations and reintroductions from captive populations would not be possible. Researchers and conservationists must recognize these dynamics when making the difficult decision to reintroduce or move populations and factor in how these dynamics may shift or affect the resident population after management. The most notable case of effective translocation and reintroduction is that of the golden lion tamarin (*Leontopithecus rosalia*). Over 30 zoos contributed 146 captive-born individuals to be reintroduced into Brazil, providing essential information on nutrition and health that aided in reintroduction strategies. Additionally, in 1994, isolated individuals in forest fragments were successfully translocated into protected regions in order to increase gene flow, which through the exchange of genes, introduces more genetic variation into the next generation (Kierulff et al. 2012).

Nongovernmental Organizations (NGOs) and Community-Based Conservation Work

Conservation NGOs have a long-standing history of working to save endangered species from going extinct. These organizations often target primates for their work because of their ability to act as umbrella species, supporting the conservation of many species found within their ecosystems. Over the past 30 years, conservation NGOs have begun to move away from a preservation-based mindset that focused on excluding humans from using protected areas. The 1990s ushered in a shift toward community-based conservation (CBC), which instead aimed to work with local people living near targeted natural environments to reduce human-wildlife conflict and establish sustainable practices (Horwich and Lyon 2007). CBC has shown success in terms of reducing hunting and deforestation in many regions including the Manas Biosphere Reserve in Assam, India, as well as in the cloud forests of Peru from the work of the Yellow Tailed Woolly Monkey Project (Horwich et al. 2012; Shanee et al. 2007). Although CBC has seen conservation successes, many warn that it should not be a panacea for all conservation goals but, rather, one mechanism among many when attempting to conserve endangered species (Reibelt and Nowack 2015; Scales 2014).

Reforestation is widely becoming one of the most practical ways in which NGOs aid in primate conservation. Organizations often collaborate with communities to establish nurseries to grow saplings, which can then be transplanted strategically to reforest certain

parts of primate habitats or create habitat corridors between forest fragments. Madagascar Biodiversity Partnership, an NGO with four field sites throughout Madagascar, has planted over 1,850,000 trees from 2010 to June of 2018 (Edward E. Louis Jr., personal communication, 05/24/2018). These efforts have been shown to be successful, as lemurs have been observed in reforested regions where they had previously not been seen.

What Can Readers of This Book Do?

It may be difficult to imagine how an individual living thousands of miles away can aid in the conservation of primates and their habitats, but in fact there are several small steps that people all over the world can take to make a difference. Many local zoos contribute to in situ conservation work as well as maintain species survival plans in order to increase diversity among zoo populations. We recommend readers visit their local zoos to learn about what actions zoos take to aid in the conservation of primates and how they can get involved in these activities.

One tangible action that can be done is to reduce the purchasing of products that contain non-sustainable ingredients. The demand for cheap oil has increased in recent years for commercial products such as peanut butter, chocolate, soaps, and shampoos, among many others. As such, palm oil plantations have expanded into wildlife habitat throughout Southeast Asia, especially in Borneo and Sumatra, the last remaining habitats of orangutans (*Pongo* spp.) and many other species of primates. This, coupled with other local pressures such as hunting and peat fires, resulted in the IUCN upgrading the Borneo orangutan's (*Pongo pygmaeus)* conservation status to Critically Endangered in 2016. They were also included in the 25 most endangered primates list for the first time (Husson et al. 2016). Although data suggest that orangutans will nest within agroindustrial environments, they will only do so with natural forest patches nearby (Ancrenaz et al. 2014). Reducing individual consumption of palm oil or choosing sustainable oil products can help reduce the overall demand; it can drive producers to commit to more environmentally friendly practices. This can hopefully slow the conversion of naturally forested landscapes into agroindustrial environments.

With the proliferation of social media, the desirability to photograph animals in close proximity has greatly increased (Pearce and Moscardo 2015). We recommend that readers who visit native primate environments resist engaging with primates in an attempt to take "selfies" with animals. Repeated encounters with travelers and tourists can overhabituate primates and put them in danger of contracting (and transmitting) diseases (Geffroy et al. 2015). Paying for photos with primates can also exacerbate the illegal pet trade because local people will be incentivized to harvest primate infants from wild populations, adversely affecting primate densities and social group dynamics. While it may be popular to try to take the most engaging "selfie" with a wild animal, it is best to just admire these animals from afar (Figure B.16).



Figure 3.1.3.1: Students on a field course observe and record data on primates in the canopy at El Zota field station in Costa Rica. Field courses are a great way to learn how to safely observe animals in the wild while gaining hands-on experience collecting behavioral, ecological, and conservation data.

Lastly, readers can aid in primate conservation by resisting sharing YouTube (or other) videos depicting primates in nonnative habitats. Often times videos of primates engaging with humans spark the popularity of these animals as pets. The desire for these animals can lead to an influx in illegal pet harvesting and trading, the mistreatment of wild animals in domestic settings, and the belief that these animals are not endangered since others own them as pets (Nekaris et al. 2013). After a video depicting a pygmy slow loris (*Nycticebus pygmaeus*) being "tickled" went viral in 2009, and another depicting a slow loris eating rice went viral in 2012, international confiscations of slow lorises increased (Nekaris et al. 2013). Awareness, coupled with the resistance to share these "cute" videos, can help reduce the market for primates to be captured for the illegal pet trade.

For those interested in gaining hands-on experience with primates, we recommend visiting Primate Info Net, where a list of field school opportunities and professional, educational, and volunteer positions are posted regularly. These listings can be found at: http://pin.primate.wisc.edu/jobs/list/avail

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3.1.4: Future Perspectives

As anthropogenic and natural disturbances continue to intensify in range and scale, the future status of the world's primates is increasingly dire. However, researchers, conservationists, and the general public are attempting to understand how primates respond to these disturbances, what actions can be done to mitigate further disturbances, how to establish sustainable relationships between humans and primates, and what small actions can be done in their own lives to aid these processes.

Regardless of our cultural or political views, we think it is valid to ask ourselves as researchers, conservationists, and students: What is the value of Earth's biological diversity, and what are our obligations to nonhuman primates, our closest living ancestors? Although scientists and conservationists often argue that there is inherent value in maintaining the world's biodiversity, we propose that primates have a special significance that goes beyond their intrinsic contribution to biodiversity. The concept that species and systems can provide a suite of benefits to humans is known as ecosystem services (Cardinale et al. 2012; Kremen 2005). These services are often classified into four categories: provisioning (e.g., food), regulating (e.g., water quality regulating), cultural (e.g., recreation and aesthetic), and supporting services (e.g., nutrient cycling) (Harrison et al. 2014; Mace et al. 2011; Millennium Ecosystem Assessment 2005). Following this approach, we propose that understanding the value of primates and their habitats in terms of their ecological, bioanthropological, cultural/historical, and economic contributions can aid in the long-term conservation of these endangered species. Recognizing the connections and continuities between ourselves and other primates is the first critical step toward caring about their future and making it part of our own.

Review Questions

- What criteria do researchers and conservationists use to identify the conservation status of primate populations and species?
- What are the main threats facing primates today, and how do the combined impacts of these threats uniquely affect primates?
- What do you think a world without primates would look like? Consider their unique significance and the various roles they play in ecology, human evolutionary and cultural history, and local economies. How would the absence of primates affect ecosystems, other animals, and humans?
- Considering all the other problems in the world today, should primate conservation be a high priority? What are the arguments to support prioritizing primate conservation?
- How can you contribute to primate conservation in your everyday life?

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