CHAPTER 5

Primate Origin

GOALS

By the end of this chapter you should understand:

1. Basic morphological features used to describe and classify fossil primates.
2. How morphological features are used to infer diet and locomotion in fossil primates.
3. Theories on primate origins.
4. General patterns of morphology and phylogenetics for fossil primates from 65 to 1.8 million years ago.

CHAPTER OUTLINE

Introduction

As an undergraduate, I was fortunate to have the opportunity to attend the annual meeting of the American Association of Physical Anthropologists. Many of the world authorities on primate origins happened to attend these meetings. As I trailed behind my academic advisor from one fascinating presentation to another, I was amazed by the enthusiasm for science exhibited by senior professors I considered to be required reading: They loved their jobs! One night I joined a throng of boisterous professors and students in the hotel lounge. Amidst the crush of bodies, I was introduced to a famous paleoanthropologist, who was carrying a mysterious large case. My advisor, who knew the old paleoanthropologist well, suggested I be shown the "new toy" from Africa. With a sparkle of humour in his eye, the old paleoanthropologist reached into his cavernous case and gently placed this "toy" in the palm of my hand. It was no toy! There, nestled ever so precariously, was the fossilized skull from a primate that was almost 33 million years old! Not only was the fossil incredibly old, it also represented a newly discovered species! Despite my nervousness at holding such a rare thing, I was fascinated by thoughts of what the creature was like when alive: what did it think about, how did it behave, did it have a mate and offspring, was it intelligent, and why did it die? I suddenly realized the sheer joy and wonder that comes from discovering a fossil primate.

In this chapter, we discuss the evolutionary anthropology of non-human primates in the fossil record. In the sections below, we undertake a broad review of primate origins from the time of the dinosaurs up until the emergence of the first hominins. Each section starts with a review of the major global patterns of geography and climate. This information is needed to understand how environmental factors influenced primate macroevolution. We then undertake only a brief review of the major morphological characteristics and ecological interpretations of the primates associated with that epoch. Finally, we piece together the phylogenetic relationships of early primates.

Introduction to Fossil Primates

Fossil primates represent a factual record of evolutionary patterns and processes over the last 65 to 80 million years. Despite the incomplete nature of these fossils, fascinating things have been learned from studies of their dental and skeletal features. We have gained invaluable insights into the diet and behaviour of fossil primates by comparing their dentition and skeletal features with those of extant primates. Therefore, we first need to cover basics of primate dentition and skeletal morphology. Macroevolutionary studies of the primate fossil record reveal intriguing evidence of intermediate forms that link extinct and extant taxa. Put differently, we find evidence for so-called missing links between some primate taxa. Thus, the fossil record provides us with information on ebbs and flows of primate diversity over tens of millions of years. Based on this information, researchers have formulated theories on how and why the first primates evolved. Finally, we review the hypothesized phylogenetic relationships of fossil primates within specific time periods. So let's learn about teeth!

Basics of Primate Dentition

Understanding basic primate dentition is important for two reasons. First, because of their extreme hardness, teeth are the most common fossilized remains found by paleoanthropologists. Second, dental morphology provides information on the diet of fossil primates. Our review focuses on dental development, tooth structure, and the kind and numbers of teeth found in primates. All primates have **diphyodonty,** meaning they have two sets of teeth. The first set of teeth, often termed "baby" or deciduous teeth, appear early in infant development, and then are replaced by a full set of

Diphyodonty ■ Having two successive sets of teeth.

Maxilla ■ Part of the upper jaw from which the teeth grow.

Mandible ■ Lower jaw.

Crown ■ The part of the tooth that is visible above the gum.

Neck ■ Part of the tooth that is within the gum line.

Root ■ Part of the tooth that is below the gum line.

Enamel ■ Outer surface of a tooth, the hardest biological substance in the body.

Cusp ■ Pointed or rounded part of the biting surface of a tooth.

adult teeth. Teeth are found in the **maxilla,** the part of the upper jaw from which the teeth grow, and the **mandible,** the lower jaw. Each tooth can be divided into the following three parts: **crown, neck,** and **root** (Figure 5.1). The tooth crown is covered by a hard substance called **enamel,** and has varying numbers and kinds of **cusps**—the pointed or rounded biting surface of the tooth. The crown is supported by dentin, which is softer than enamel. The pulp cavity underlies dentin, and forms the central chamber of the tooth. Pulp comprises soft tissue, blood vessels, and nerves that provide sensitivity to heat and cold.

All primates are characterized by **heterodonty,** meaning they have different kinds of teeth (Figure 5.2). Specifically, most primates have the following four kinds of teeth (from front to back): **incisors, canines, premolars,** and **molars**. These teeth can be categorized into two parts: anterior dentition (incisors and canines) and posterior dentition (premolars and molars). Paleoanthropologists use the dental formula to describe the number of each kind of tooth in one half of the maxilla and mandible of a species. Why only one half? Because primate morphology is the same on the left and right sides. For example, the dental formula for modern humans in 2.1.2.3./2.1.2.3., which means that you should have a total of four incisors, two canines, four premolars, and six molars on the left or right side of your mouth. In primates, such as humans, that also have symmetrical upper and low dentition, it is common to see the dental formula listed only as 2.1.2.3.

Heterodonty ■ Different kinds of teeth.

Incisors: front teeth between the canines

Canines: front teeth between the canines

Premolars: cheek tooth found between canines and molars

Molars: Teeth posterior to the premolars.

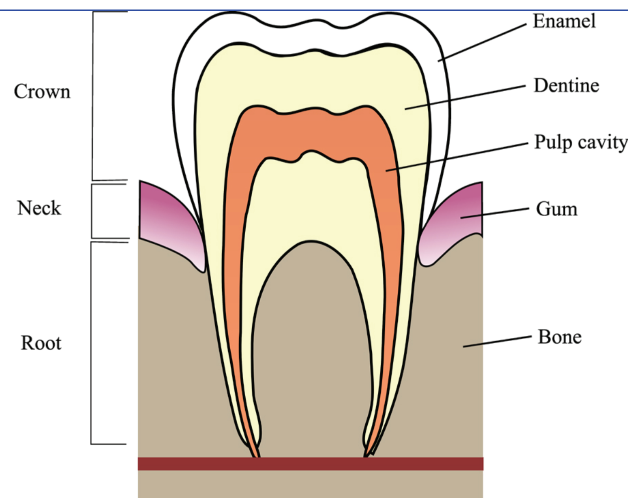

Figure 5.1

Basic tooth anatomy of an adult molar tooth in a modern human.

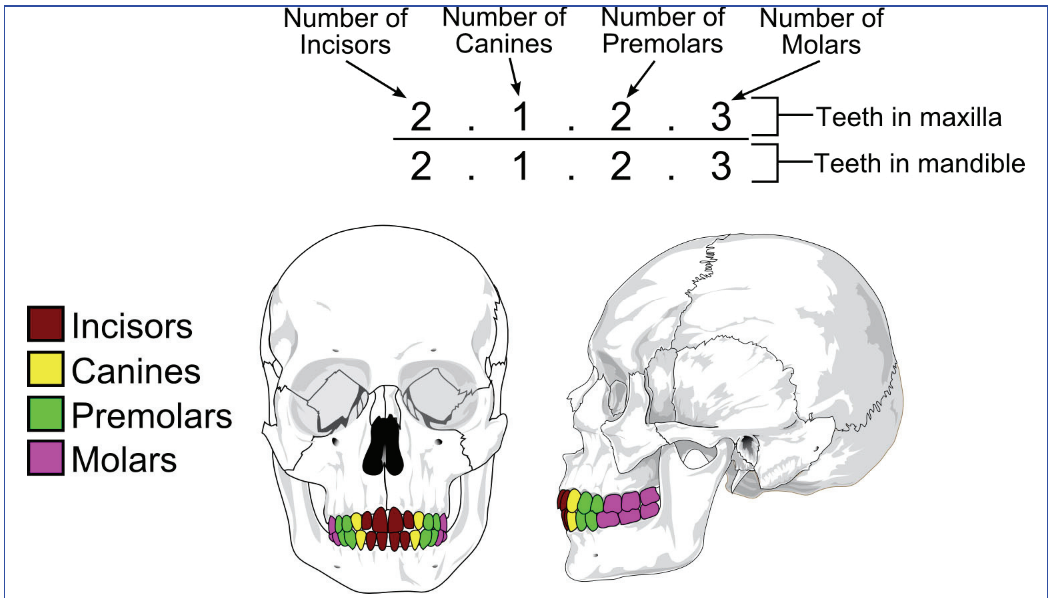

Figure 5.2
The dental formula and the different kinds of teeth in an adult human. © *S. M. Lehman*

Basics of the Primate Skeleton

We now look at the basic anatomy of the **cranial** and **postcranial skeletons** of primates. This introduction to the bones of the head and below the head is also necessary as a foundation for understanding the diet and locomotion of fossil primates. We'll do a broad overview because it is extremely rare for a complete primate skeleton to be fossilized and recovered. In most cases, all that is found are a few cranial fragments, and in even rarer cases, parts of the postcranial skeleton. We start at the top (skull) and work our way down.

Cranial skeleton ■ Bones of the head.

Postcranial skeleton ■ Bones below the head.

In primates, the adult skull is composed of numerous bones of varying shapes and sizes that encase the brain, sensory organs, and mastication (chewing) system (Figure 5.3). As we discussed above, the mandible and maxilla are part of the cranial skeleton. However, only the mandible and a few bones of the inner ear are unfused and capable of movement. The other cranial bones fuse together to form the cranium or brain case. The top of the cranium is composed of the following three bones: frontal (forehead), parietal (side), and temporal (temple). The occipital bone forms the back and bottom parts of the cranium. The foramen magnum is an opening in the occipital bone through which passes the spinal cord. The zygomatic bone (cheekbone) is another important anatomical feature in paleoanthropology.

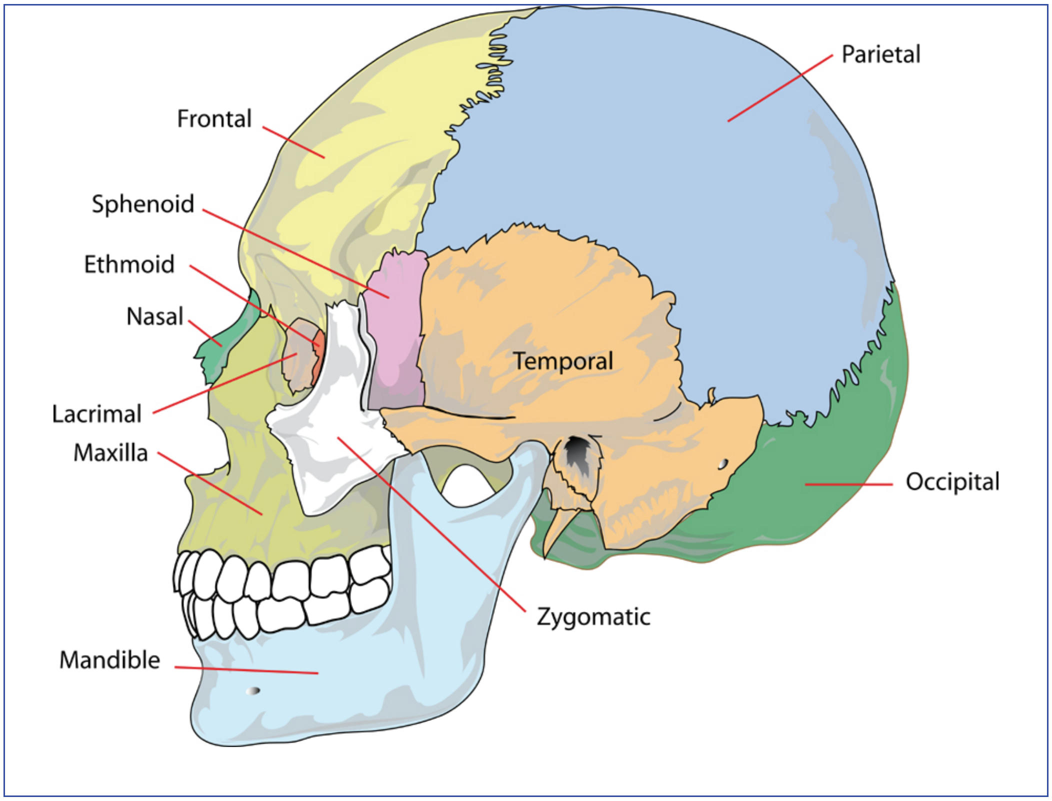

Figure 5.3
Basic skeletal anatomy of a skull in an adult, modern human.

Postcranial Skeleton and Locomotion Although the postcranial skeleton serves numerous functions, we focus our basic introduction on skeletal features associated with locomotion (Figure 5.4). In this regard, the primate skeleton can be divided into three parts: the axial skeleton, the forelimbs, and the hindlimbs. The axial skeleton is composed predominantly of the vertebrae and ribs. For the forelimb, we focus on the clavicle (collarbone), humerus (upper arm bone), radius and ulna (forearm bones), and the phalanges (finger bones). For the hindlimbs, we are mainly interested in the pelvis or pelvic girdle, femur (thighbone), tibia and fibula (shinbones), and the phalanges (toe bones). With these basics of primate anatomy, we can now look at how paleoanthropologists make functional hypotheses on what fossil primates were like.

How Do We "Know" What Fossil Primates Were Like?

One of the (many) things that puzzled me as a student was how paleoanthropologists could look at a few fragments of bone—or even one tooth—and then describe general aspects of the body mass, diet, and behaviour of a fossil primate. After all, unlike studies of extant primates, it's not possible to observe fossil primates in their natural environments. Instead, paleoanthropologists use the comparative method to understand morphological adaptations in fossil primates. The comparative method, as it applies to palaeoanthropology, is based on inferences gleaned from studies of form and function in extant primates. Paleoanthropologists look at the relationship between, for example, certain dental characteristics and diet in extant primates. If a similarly sized extinct primate exhibits the same dental characteristics as those seen in a well-studied extant species, then the researcher hypothesizes that the animals must have eaten the same kinds of food. For example, insect-eating primates, such as tarsiers, are characterized

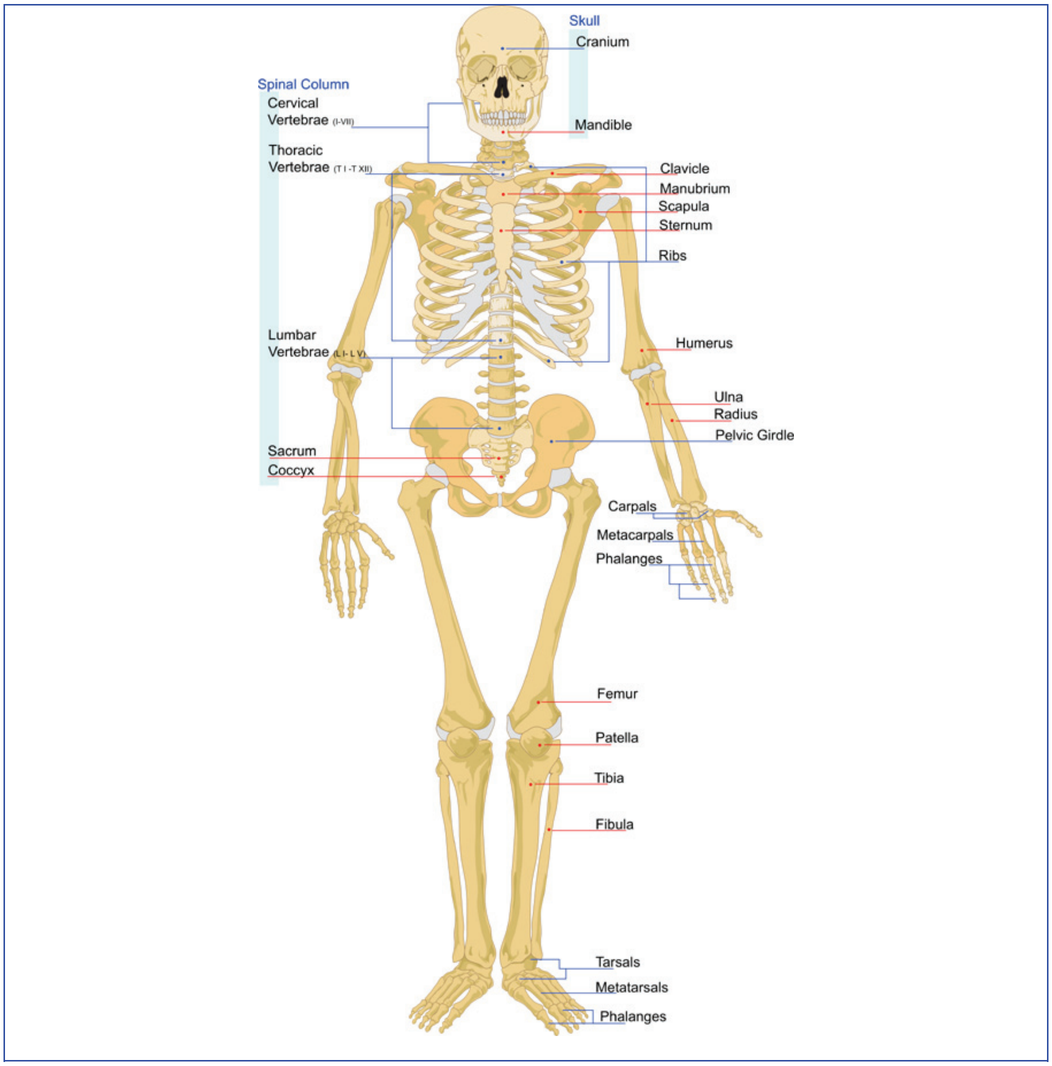

Figure 5.4

Basic postcranial skeletal anatomy in a modern human.

by having short, sharp cusps on their teeth, which serve to crush the often hard outer shell of insect prey. If a similarly sized fossil primate has the same overall teeth shape and size as tarsiers, then researchers infer that the diets were likely similar. This process can also be applied to studies of the postcranial skeleton and locomotion in fossil primates. Following, we look at some of the main morphological indicators of body mass, diet, and locomotion in fossil primates.

Body Mass in Fossil Primates A fundamental issue in paleoanthropology is determining the body mass of fossil primates. This information is important because body mass relates to many aspects of the biology, behaviour, and ecology in primates (see Chapter 4). To determine body mass, paleoanthropologists employ a statistical procedure known as **correlation,** which refers to the relationship between variables. Many features, such as the cross-sectional area of molars, are positively correlated with body mass. In other words, large-bodied primates tend to have relatively large teeth. Paleoanthropologists hypothesize that correlates to body mass in extant primates also hold for extinct primate taxa. Thus, the recovery of a few teeth from a fossilized primate can provide sufficient data to make a rough estimate of its body mass. Teeth tell us much more than just how much a fossil primates weighed, as we see next.

Correlation ■ A statistical relationship between two variables such that high values on one factor tend to go with high values on the other factor.

Dental Correlates to Diet in Fossil Primates We look at two morphological aspects of dentition as they pertain to diet: enamel thickness and dental morphology. First, interspecific variations in enamel thickness tend to reflect differences in the physical properties of foods eaten by primates. Species with a diet composed of hard, gritty food, such as seeds, tend to have thick enamel whereas species such as folivores that eat leafy plant foods tend to have thin enamel. Second, although the anterior dentition of many primates serves non-dietary functions, such as grooming and defence, it does serve in the initial preparation of food for **mastication** (chewing). The strongest functional signal for incisors and canines is seen in primates that use their teeth on bark, wood, and fruit. In other words, researchers can best interpret the use of incisors and canines in primates that use these teeth to acquire or chew food. Primates that open bark and wood to get at insects and plant exudates tend to have **procumbent** (forward-projecting) incisors. Frugivorous primates often have relatively larger, broader incisors than those seen in folivores. This pattern exists because a frugivore first bites into its food using the anterior dentition, just like most people do when eating an apple or even peeling the rind off an orange. However, anterior dentition also serves social and defensive roles, including threatening open-mouth displays and biting. As a result, it can be difficult to separate dietary and socioecological roles for anterior dentition in fossil primates. Conversely, posterior dentition has a stronger dietary component than anterior dentition. A primate that eats leafy materials passes the food directly to its premolars and molars. In other words, it’s easier to chew up salad using your posterior dentition than your incisors and canines. For folivores, the combination of thin enamel and sharp, pointy cusps enables them to efficiently slice leaves, just like a pair of scissors. Insectivorous primates also have sharp cusps on their teeth, but not necessarily thin enamel, because they must cut through the hard outer body parts of insects to get to the soft, yummy insides. The molars of frugivores tend to have low, rounded cusps (called *bunodont*), which serve as a broad basin for masticating fruit pulp. Other clues to the diet of extinct primates can be found on their cranial skeleton.

Mastication ■ Chewing of food.

Procumbent ■ Teeth that project forward.

Cranial Correlates to Diet and Locomotion in Fossil Primates The cranial skeleton is unique because it provides information on both diet and locomotion in fossil primates. The most important dietary aspect of cranial morphology involves features associated with chewing. Chewing is achieved predominantly by the actions of the following four muscles: masseter, temporalis, medial pterygoid, and lateral pterygoid. Each of these muscles connects the mandible to various parts of the skull. To find one of these muscles, place your fingers on your temple the next time you are chewing. You will feel the temporalis muscle twitching under your skin. As you chew, slowly move your fingers up to the top of your skull. At a certain point, you will notice that you no longer feel the twitching muscle. This point marks the origin of the muscle on your skull, which then terminates or inserts on the top of your mandible. Paleoanthropologists can look at the size and location of the muscle attachments on the skull and mandible to gain information on the relative bite force involved in mastication. Primates that feed on hard objects, such as tough seeds or fibrous plant parts, tend to have larger muscles and muscle attachments on their skull and mandible.

Cranial anatomy and morphology also provide information on the activity patterns and locomotion of extinct primates. Information on activity patterns can be determined by looking at the relative size of the eye orbits compared to the overall size of the skull. Nocturnal primates tend to have relatively larger eye orbits compared to their skulls, whereas diurnal primates usually have relatively smaller eye orbits compared to the crania. Paleoanthropologists also look at the location of the foramen magnum to approximate body posture and locomotion (Figure 5.5). In quadrupedal primates, the foramen magnum tends to be placed more at the back of the head, indicating a prone body posture. In upright primates, such as bipedal humans, the foramen magnum is located directly under the skull.

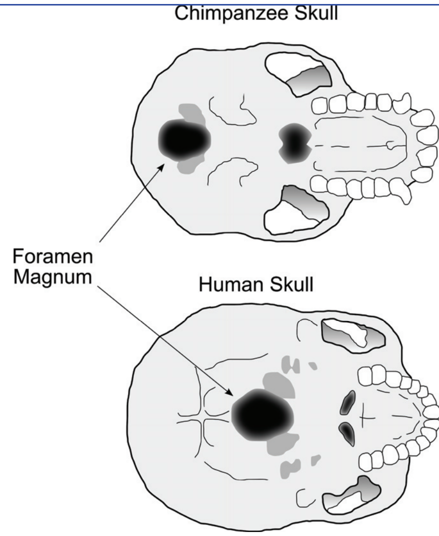

Figure 5.5

Graphical representation of the base of the skull in a modern chimpanzee and human.

In the human, the foramen magnum is located in a more anterior (frontal) position than in the chimpanzee. Note that the skulls are not drawn to scale. © *S. M. Lehman*

Postcranial Correlates to Locomotion in Fossil Primates The postcranial skeleton can be examined to deduce the locomotor behaviour of extinct primates. We focus on basic postcranial features associated with the following four common locomotor patterns utilized by primates: arboreal quadrupedalism, terrestrial quadrupedalism, leaping, and suspension. We discuss bipedalism in Chapter 6. Arboreal quadrupeds tend to have a narrow axial skeleton, long tails, moderately long digits, and short forelimbs and hindlimbs of equal length. These primates tend to be in a constantly flexed position (i.e., bent knees and elbows). Consequently, the elbows and knees of arboreal quadrupeds exhibit specific adaptations to support the animal in a flexed posture. These adaptations and body posture lower the centre of gravity of an arboreal quadruped, which enhances stability and balance on an inherently unstable **substrate,** or surface (i.e., tree branches). For example, perhaps you recall playing as a child on a playground tightrope or walking along a fence or wall. Your first reaction to any destabilization of the substrate was to crouch down, thereby lowering your centre of gravity and, hopefully, regaining stability. Otherwise, you were likely to fall to the ground.

Substrate ■ Surface on which an organism moves.

The limbs of terrestrial quadrupeds are built more for speed than for stability. The forelimbs and hindlimbs are long and tend to be held in an extended position. Terrestrial quadrupeds also tend to have a short tail and digits. In leaping primates, numerous postcranial features are associated with strong propulsive forces needed by the animals to jump. We focus on one main feature, which is their long hindlimbs. In fact, leapers tend to have much longer hindlimbs than forelimbs. Interestingly, they also have a narrow tibia, which likely reflects the simple hinge-like flexion and extension used by the animals during a leap. Conversely, suspensory primates have longer forelimbs than hindlimbs. Their hips and shoulders are very mobile, ensuring they can grasp a wide array of constantly changing support structures. They also tend to have very long, curved fingers, which are used to hook onto a branch. Most suspensory primates lack a tail.

You should note that the above morphological descriptions represent only a small proportion of the information used by paleoanthropologists to reconstruct the behaviour and ecology of fossil primates. Nonetheless, we can now turn to theories on how and why primates evolved.

Theories on Primate Origins

Just as we're intrigued by the question of human origins, paleoanthropologists are fascinated by questions on when and why the first primates evolved. In fact, these questions are interrelated because humans are descendants of the first primates. However, there is considerable controversy regarding primate origins. Put differently, we don't yet know the evolutionary relationships among the first primates, their descendants, and other broadly contemporaneous mammals. Despite this question, researchers have formulated numerous theories on why primates evolved in the first place. Of these, the most widely accepted encompass three slightly different views on primate origins: arboreality, predation, and ecology.

Fred Szalay (1972) originated the arboreal theory of primate origins. In this theory, primate origins represent an adaptive radiation of new species from early arboreal mammals. The impetus for this evolutionary shift was a change in diet from insectivory to herbivory. Grasping hands and feet also evolved in these early mammals to facilitate moving about in the complex web of flexible tree branches. Although this theory accounts for changes in dentition and limb morphology, it fails to explain certain aspects of the primate visual system. Specifically, why do other arboreal mammals lack the orbital convergence and stereoscopic vision exhibited by primates and visual predators, such as owls and hawks?

Thus, Mart Cartmill (1992) came up with an alternative idea on primate origins, the visual predation theory. In this theory, primate origins can be traced back to visual adaptations for hunting prey in arboreal habitats. Cartmill also suggested that arboreal hunting resulted in the evolution of grasping hands and nails, rather than claws, to capture and hold prey in small, terminal branches. Despite explaining a broader suite of primate characters, Cartmill's theory has not been supported by detailed ecological studies of insectivorous primates. Specifically, nocturnal insectivores are more likely to hunt using smell and sound rather than sight (Wright et al., 2003). Furthermore, field studies revealed that tamarins, which have claw-like nails, are adept at both hunting for insects in terminal branches and clinging to tree trunks to feed on exudates (Garber, 1980).

These observations led, in part, to Robert Sussman's (1991) more ecologically based idea on primate origins, called the angiosperm co-evolution theory. Sussman suggested that the major impetus for primate origins and adaptations was the roughly contemporaneous evolution of angiosperm plants, which produced tasty and nutritious fruit in their terminal branches. However, field studies of extant mammals similar to those that led to the first primates failed to provide conclusive evidence in support of either Sussman's or Cartmill's theories (Rasmussen, 1990). In fact, field studies provide support for aspects of both theories. Therefore, the incomplete fossil record, particularly during the earliest stages of primate evolution, makes it impossible to determine which of the above theories is correct. These issues reveal exciting research and career opportunities for students just like you.

Ecosystem and Temporal Aspects of Primate Origins

Dinosaurs were the dominant vertebrates from about 230 to 65.5 million years ago (MYA), at which point the fossil record indicates a mass extinction of dinosaurs, reptiles, and plants in both terrestrial and aquatic environments. Although the causes of this mass extinction are hotly debated, the prevailing theory is that a massive asteroid impact threw up a long-lasting, worldwide layer of debris, thereby blotting out sunlight and disrupting plant growth. The loss of plant species caused an extinction cascade of herbivores and their predators in many parts of the planet. For reasons that are poorly understood, some mammal and bird lineages survived this mass extinction event. This information dispels the common misconception that mammals evolved after the extinction of dinosaurs. In fact, mammals evolved from cynodonts (mammal-like dinosaurs) about 220 MYA. Thus, mammals were already an ancient lineage by the time the dinosaurs went extinct. The Cenozoic Era, which began about 65.5 million years ago and continues through today, marks the end of the "Age of the Dinosaurs" and the beginning of the "Age of the Mammals." An **era** is one of 11 geologically determined and clearly defined periods of time. This geological period is, therefore, particularly relevant to primate origins and evolution. There were considerable geological and climatic changes during the Cenozoic (Figure 5.6). The Cenozoic is subdivided into the following epochs: Paleocene, Eocene, Oligocene, Miocene, Pliocene, Pleistocene, and Holocene (Table 5.1). An **epoch** is a span of time smaller than an era. We start with the Paleocene, and then work our way forward in time to the Pliocene. We'll cover the Pleistocene and Holocene in the next chapter on hominin origins.

Era ■ One of approximately 11 units of geological time that cover the ca. 4.6-billion-year age of Earth (e.g., Cenozoic Era from 65.5 millions of years ago to present).

Epoch ■ A unit of geological time that is a subdivision of an era.

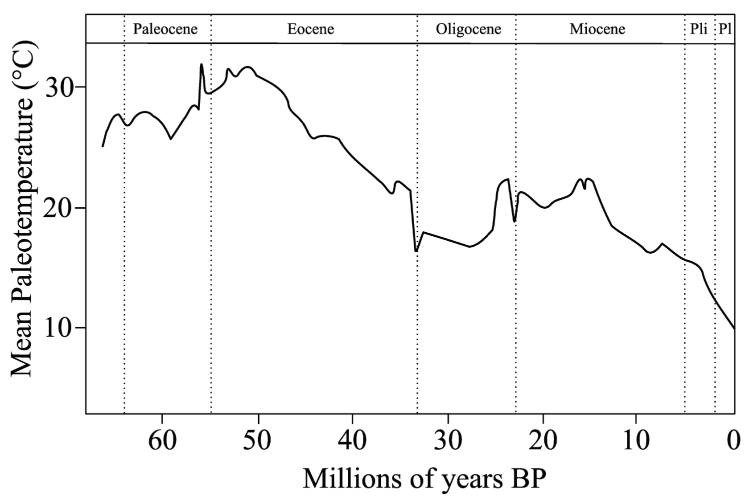

Figure 5.6
Changes in temperature during the Cenozoic era.

TABLE 5.1

EPOCHS OF THE CENOZOIC ERA

Epoch	Start (MYA)	End (MYA)
Holocene	0.01	On-going
Pleistocene	1.80	0.01
Pliocene	5.33	1.80
Miocene	23.03	5.33
Oligocene	33.90	23.03
Eocene	55.80	33.90
Paleocene	65.50	55.80

Paleocene "Primates"

The Paleocene epoch lasted from 65.5 to 55.8 MYA. Compared to the present-day world, global geography was very different during the Paleocene. North America, South America, Africa, and India were island continents; much of Europe and western Asia were inundated with water; and Australia had only just separated from Antarctica. The global climate also differed markedly from present-day conditions, in that the world was a considerably warmer and wetter place. Much of the Northern Hemisphere and parts of the Southern Hemisphere had a warm, temperate climate. Greenland and Antarctica had cool, temperate climates, which is very different from their current frigid conditions. Central Africa and parts of southern Asia had hot, tropical climates, just as they do today. Tropical forests covered much of central Africa and southern Asia, whereas temperate forests covered much of North America, Europe, and eastern Asia. Regions formerly covered in temperate forests now contain some of the best sites for locating Paleocene mammals. In fact, each year there are opportunities for students, just like you, to join paleoanthropologists in looking for Paleocene mammals in places like Utah and Wyoming. What did Paleocene mammals look like and do?

Paleocene Mammals: Any Primates Here?

Palaeontologists have found fossilized remains of Paleocene mammals, including rodents and bats, in various parts of the world. Of these mammal fossils, some remarkably primate-like taxa, best represented by a group known as Plesiadapiformes (Figure 5.7), have been found in North America, Europe, and Asia. Plesiadapids ranged in body mass from 7 to 3000 g. They had a primitive dental formula of 3.1.3.3. Their cranial remains indicate a nocturnal activity pattern in that relative to their overall body size, plesiadapids have eye orbits that are quite large. Based on studies of their dentition, paleoanthropologists are confident that most plesiadapids ate seeds and insects. Analysis of the few postcranial remains suggests an arboreal, scampering mode of locomotion similar to that seen in squirrels.

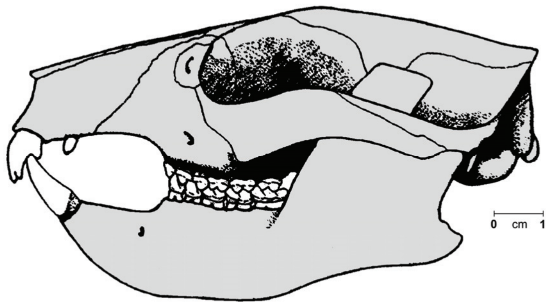

Figure 5.7

Plesiadapis skull.

Note the rodent-like incisors and lack of postorbitol closure in this early mammal. © *S. M. Lehman*

Phylogenetic Relationships among Paleocene "Primates"

As a student, I always wondered why scientists got excited each time some new fossil was found. After all, it's just one fossil, right? The reason for this excitement is that due to the paucity of quality fossils of Paleocene mammals, particularly those with primate-like features, the addition of even one new specimen can alter interpretation of primate origins. If paleoanthropologists have only the anterior dentition of a fossil primate, then their interpretations of its life ways can be changed by the discovery of posterior dental remains. It should come as no surprise to you that our idea of primate phylogeny during the Paleocene has changed over the years. Up until about 40 years ago, plesiadapids were classified as primates because of certain aspects of their teeth and because their limbs were adapted for an arboreal lifestyle. More recent investigations indicate that plesiadapids are unlikely to be members of the Primate Order because they retain the following primitive mammalian traits: no postorbital bar, claws instead of nails on their digits, eyes placed on the side of the head, and greatly enlarged incisors. However, genetic research places the timing of primate origins at about 85 MYA (Springer et al., 2003), well before the start of the Paleocene epoch. Thus, we either haven't found any primate remains from the Paleocene epoch or interpretations of a few cranial characters in Plesiadapids are flawed. A possible answer to this long-standing issue can be found in a recent study on primate origins (Bloch et al., 2007). Specifically, a cladistic analysis of newly discovered and beautifully preserved Paleocene mammals indicates that plesiadapids, and a few other contemporaneous mammals, are sister taxa to primates of modern aspect, known as the Euprimates. Put differently, if this cladistic analysis holds up to scientific scrutiny, then Plesiadapiformes are, in fact, in the Primate Order. In the following section, we look at Euprimates of the Eocene epoch.

Eocene Primates: Are We There Yet?

During the Eocene epoch (55.8–33.9 MYA), the continents continued to move, albeit incredibly slowly because of **plate tectonics:** the plates of the Earth's crust move, resulting in changes to the position, size, and shape of continents and oceans. South America and Africa were still island continents, as was North America during the early parts of the Eocene. The main differences in paleogeography involved land bridges between the major continents. For example, early in the Eocene there was a connection between North America and Europe, as well as between Asia and Europe. Over the next few millions of years, these connections were lost, resulting in divergence of the various mammals on each continent. These global patterns of continental geography contributed to some of the most extreme climatic conditions of the Cenozoic Era. The global climate was extremely warm and wet during the early parts of the Eocene, followed by a slow reduction in temperature and humidity for the remainder of the epoch. Consequently, warm, temperate forests expanded into polar regions. Although many lineages of modern mammals, such as **ungulates** (hoofed mammals), evolved during the Eocene, most were typically smaller in body size and mass than extant forms. Fossil deposits dated to this epoch also provide the first evidence of primates similar in form to extant strepsirhines. Moreover, we have the first tantalizing evidence of monkey-like primates. Clearly, the Eocene was an ideal time to be a mammal.

Plate tectonics ■ Geological theory that the plates of the Earth's crust move, resulting in changes in the position, size, and shape of continents and oceans.

Ungulates ■ Mammals with hooves (e.g., horses, deer, sheep).

Finally, the First "Modern" Primates!

Some fossil mammals recovered from Eocene deposits exhibit morphological features similar to those seen in extant strepsirhines and even one special group of haplorhines. Specifically, these mammals have a postorbital bar and nails instead of claws. Because of this abrupt morphological transition from the more primitive features of Plesiadapiformes of the Paleocene, the primates of the Eocene are often categorized as **Euprimates,** meaning that they look very much like some modern primates. Based on suites of unique characters, most Eocene primates are typically divided into four taxonomic groups: the Adapoidea (adapoids), Omomyoidea (omomyoids), Eosimiidae (eosimiids), and Oligopithecidae (oligopithecids).

Euprimates ■ Primates of modern aspect.

Adapoidea: Ancestral Lemurs? Adapoids were common to the Paleocene animal communities in North America and Europe, but relatively rare in Asia and Africa. Paleoanthropologists have described approximately 116 species of adapoids, with more being dug up each year. Body mass estimates for adapoids range from 100 g up to 6900 g, which makes this taxon similar in size to extant strepsirhines. Most adapoids had small eye orbits indicative of a diurnal lifestyle, a long snout, and a primate-like dental formula of 2.1.4.3. They also had small incisors and large canines. The dental morphology of these early primates indicates that they were folivores and frugivores, marking an important dietary transition in primate evolution. Adapoids had long legs as well as a long body and tail. Although some adapoids exhibit peculiarities in their postcranial morphology, most taxa had movement patterns that likely ranged from quadrupedal running and leaping in small-bodied forms to leaping in larger-bodied taxa. Thus, adapoids exhibit a lemur-like suite of morphological features.

Omomyoidea: Ancestral Tarsiers? Eocene omomyoids first appeared in North America, Europe, and Asia (Figure 5.8). Like the adapoids, there were numerous species of omomyoids, particularly in North America. These primates ranged in body size from 45 to 2500 g, although most weighed less than 1000 g. Thus, omomyoids were somewhat smaller in body mass than adapoids. Omomyoids were characterized by having large eyes, indicating a nocturnal activity pattern, and short snouts. They had large in-

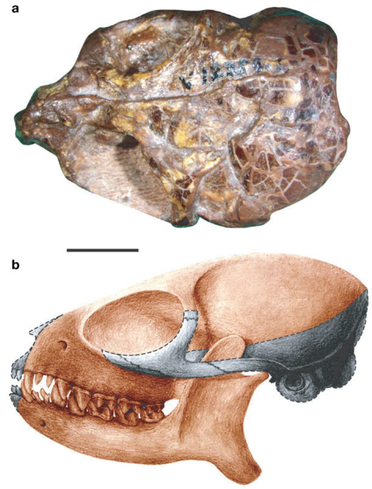

Figure 5.8

Top view of fossilized skull (a), and artist's reconstruction of the skull (b), from an Omomyoid primate, *Teilhardina*.

Note the post-orbitol bar in this specimen. Scale bar equals 5 mm.

Adapted by permission from Macmillan Publishers Ltd: NATURE (427, 65–68), © 2004.

cisors and small canines. Taxa in the early Eocene had a dental formula of 2.1.4.3, whereas latter taxa lost one of their premolars, resulting in a dental formula of 2.1.3.3. Their dental morphology indicates interspecific variations in diet, ranging from insectivory in small-bodied forms to frugivory and even folivory in larger-bodied taxa. Omomyoids were predominantly arboreal leapers and quadrupeds. A few species exhibit a partially fused tibia-fibula, like that seen in extant tarsiers. Therefore, omomyoids exhibit a tarsier-like suite of morphological features.

Eosimiidae and Oligopithecidae: Ancestral Haplorhines? Paleoanthropologists have recovered some fragmented jaws, loose teeth, and a few postcranial bones of Eocene primates from China and Egypt. Those from China are placed in the Eosimiidae family and those from Egypt are in the Oligopithecidae family. Eosimiids were rather small creatures, weighing about 100 g. They have a platyrrhine-like dental formula of 2.1.3.3., with small, spatulate incisors and broad premolars and molars. The postcranial material hints at monkey-like properties. The oligopithecids weighed about 900 to 1500 g. Surprisingly, oligopithecids have a 2.1.2.3. dental formula, just like in modern catarrhines (Old World monkeys and apes). Moreover, their cranial morphology, such as the shape of the auditory bulla , bears some remarkable similarities to extant Catarrhines. The diet of oligopithecids was probably composed of insects and leafy materials. Hopefully, future expeditions will recover additional eosimiids and oligopithecids because little functional or phylogenetic information can be obtained from the currently assemblage of fossils.

Phylogenetic Relationships among Eocene Primates

A fundamental issue in primate evolution is resolving phylogenetic relationships in Eocene primates. Why? Because these mammals are the first to be definitively identified as members of the Primate Order (Figure 5.9). Thus, they represent, at this time, the most likely common ancestor for all extant primates. Moreover, paleoanthropologists are seeking answers to the following fascinating questions: Are adapoids the first strepsirhines, and are omomyoids the first tarsiers? Part of the issue with resolving issues of primate origins in the Eocene is that some taxonomists use only a few, obvious morphological features to define each taxonomic group (e.g., size of eye orbits). Recall from the previous chapter that this kind of scientific debate fails to resolve phylogenetic relationships between taxa. On the other hand, cladistic studies of primates from the Paleocene and Eocene led to the formulation of three hypotheses on primate origins. First, this research supports adapoids and omomyoids as separate primate lineages. Second, adapoids and strepsirhines form a distinct group, as do omomyoids and haplorhines. Finally, there is support for haplorhines to have evolved from omomyoids. However, the recent discoveries of unique adapoids and omomyoids in Asia and Africa means that the above three points should be viewed only as hypotheses, which paleoanthropologists will test and revise in the future.

One of the most hotly debated issues in primate evolution involves the phylogenetic relationship of eosimiids and oligopithecids to other primates. The highly fragmented remains of the eosimiids make it difficult to conduct phylogenetic analyses because doing so can result in erroneous conclusions that are eventually refuted by the discovery and analysis of more complete fossil specimens. For example, some dental features of the Eosimiidae point to a broad haplorhine relationship, whereas others indicate a close phylogenetic relationship to tarsiers. Although most specimens of oligopithecids tend to be better preserved, their unique combination of primitive and derived features has made it difficult to resolve the phylogenetic relationships of this taxon to other Eocene primates as well as those found in Oligocene deposits. More eosimiids and oligopithecids must be found and analyzed before any definitive phylogenetic assessments can be made. At present, all that can be said is that the discovery of the eosimiids and oligopithecids may push haplorhine origins as far back as the Eocene. Definitive haplorhines are not known until the Oligocene.

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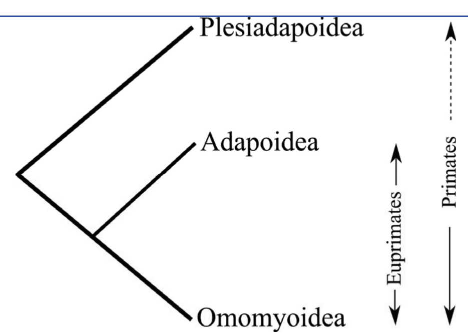

Figure 5.9

Phylogenetic relationships of Eocene primates.

Inclusion of Plesiadapids in Primates indicated by dotted line, follows recent work by Bloch et al., 2007.

Oligocene Primates: Hey, Is It the Monkeys?

The transition from the Eocene to the Oligocene (33.9–23.0 MYA) marked continued changes in global geography, climate, and primate habitats. The continents were located close to where they are today, except that there was no land connection between North and South America. Perhaps the most important geological change was the separation of South America and Australia from Antarctica, which resulted in major changes in ocean currents around the newly frozen South Pole. Consequently, there was a major drop in global temperatures and sea levels, which greatly reduced the extent of forest cover, particularly in the Northern Hemisphere.

Morphological Features of Oligocene Primates

Although many Euprimates disappeared from North America and Europe, new primate taxa evolved in Asia, Africa, and South America. Most importantly, these new taxa exhibit some morphological features similar to those seen in extant monkeys rather than strepsirhines. Most Oligocene primates can be divided into the following three taxonomic groups within the Haplorhini suborder: Parapithecidae, Propliopithecidae, and Platyrrhini. Fragmentary remains of quite a few fossil taxa have, so far, defied attempts to be taxonomically classified. What is it about these fossil primates that indicates they were monkeys rather than lemurs or, for that matter, apes? No single feature can unite Oligocene primates with extant monkeys. Rather, many of these fossil taxa have most but not necessarily all of the main diagnostic features of monkeys. These features include full postorbital closure, a 2.1.3.3. or 2.1.2.3. dental formula, and derived aspects of the molar and skeletal morphology, which we don't cover in this text. However, other morphological aspects of Oligocene primates are unique and differ from those seen in extant monkeys. Below, we take a closer look at these three groups of Oligocene primates.

Parapithecidae Much our information on Oligocene primates comes from long-term excavations at the Fayum Depression in Egypt. The Fayum is a remarkable geological outcrop of Eocene-Oligocene deposits surrounded by desert. Although present conditions are uniformly hot and dry, 34 MYA this area was covered in tropical swamps that contained a remarkable array of plants and animals, including ancestral manatees, rhinos, and primates. The Parapithecidae have been found in late Eocene to early Oligocene deposits. This fascinating primate family contains 8 to 10 species, which ranged in body mass from 300 to 3000 g. Although their dental formula of 2.1.3.3. is just like that seen in extant Platyrrhines, other dental features indicate affinities with both lemurs and monkeys. In parapithecids, the mandible symphasis is fused, as in modern monkeys. Of the few cranial remains recovered to date, all exhibit relatively small eye orbits and full postorbital closure. Other cranial and postcranial skeletal features are like those seen in modern platyrrhines. Parapithecids were likely to have been diurnal frugivores and excellent leapers.

Propliopithecidae Propliopithecids have been found in early Oligocene deposits at the Fayum. Although propliopithecids share certain haplorhine features with contemporaneous parapithecids, such as a fused mandibular symphasis and postorbital closure, there are some important morphological differences between the two families. Propliopithecids were larger in size, with species-specific estimates of body mass ranging from 900 to 6700 g. They had a dental formula of 2.1.2.3., like that seen in modern Old World monkeys and apes (Figure 5.10). Propliopithecids have an ape-like arrangement of five molar cusps, rather than the bilophodont molars common in modern catarrhine monkeys. The recent discovery of a complete cranium from *Aegyptopithecus,* the best known propliopithecid, reveals two rather startling things about its brain

Figure 5.10

Skull from a *Aegyptopithecus zeuxis*.

Count the number of teeth and you'll see that this early primate shares our dental formula (2.1.2.3.).

© S. M. Lehman

size and intersexual size differences (Simons et al., 2007). First, the brain-to-body size ratio was similar to that found in extant lemurs, indicating that the evolution of large brain size had not yet occurred in Oligocene catarrhines. Second, there was considerable sexual dimorphism in this taxon. Postcranial remains of *Aegyptopithecus* are more primitive than modern catarrhines but more advanced than extant strepsirhines. Studies of the cranial and postcranial morphologies of *Aegyptopithecus* indicate that it had a diurnal activity pattern, frugivorous and folivorous diet, and was an arboreal quadruped.

Fossil Platyrrhines Researchers have unearthed Oligocene primates in South America, which at that time was an island continent. These discoveries are remarkable because no primates have been recovered from earlier epochs in the Neotropics, indicating that the origin of these early platyrrhines lies outside South America. So how did these early platyrrhines get to South America? Despite years of scientific speculation, the prevailing theory is that some unknown Oligocene primate rafted over from Africa. Models of continental geography indicate that Africa and South America were closer together during the Oligocene epoch and that ocean currents flowed quite strongly in a westerly direction between these continents. Thus, some small-bodied primates are thought to have survived a few weeks eating insects and fruit on a large tree across the Atlantic Ocean from Africa to South America. Yes, that's the best we can come up with!

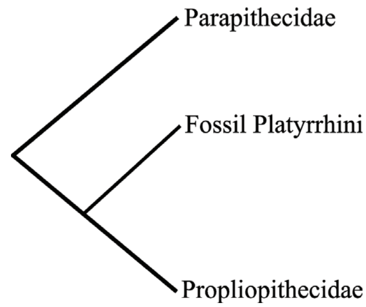

Figure 5.11

Phylogenetic relationships of Oligocene primates.

What do we know about these monkeys? The earliest platyrrhines were small monkeys weighing about 500 to 1000 g. Although they have the characteristic platyrrhine dental formula of 2.1.3.3., the low, rounded cusps on their teeth are similar to those seen in some primate fossils from the late Eocene in the Fayum region of Egypt. Paleoanthropologists conclude that these early fossil platyrrhines were frugivores. Few cranial and no postcranial remains have been recovered, which limits any theories on the activity and locomotor patterns of fossil platyrrhines from the Oligocene.

Phylogenetic Relationships among Oligocene Primates

Phylogenetic analysis of Oligocene primates has resulted in more debate than consensus on their evolutionary relationships. Because the remains are fragmentary and the vast majority of Oligocene fossils come from only a few sites in Africa and South America, a conservative approach is needed to summarize their phylogenetic relationships. What we can say here is that there is general support for the parapithecids being ancestral to a clade forming the propliopithecids and the fossil platyrrhines (Figure 5.11). Put differently, propliopithecids share a more recent common ancestor with each other than either does with the parapithecids. As with earlier epochs, we desperately need students like you to unearth Oligocene primates from new sites. Only with these additional specimens will paleoanthropologists be able to start sifting through the bewildering array of hypotheses on evolutionary relationships among fossil lemurs, Old World monkeys, and New World monkeys.

Miocene Primates: Planet of the Apes

The Miocene epoch, which lasted almost 18 million years (23.0–5.3 MYA), marks the evolution of primitive apes. The main paleogeographic feature relevant to primate origins involved cycles of expansion and reduction in the size of primate habitats in the Mediterranean and Eurasia. Land bridges formed and disappeared between Africa, Europe, and Eurasia. During the early stages of the Miocene, the climate was similar to today's conditions, but warmer. About 15 MYA, the climate became considerably cooler and drier as glaciers formed in Antarctica. Consequently, tropical forests transitioned to a mosaic of woodland savannah (trees and grass) and savannas (grass). This cooling also resulted in the expansion of savannah-woodland environments in Africa and Eurasia. During this time, Old World monkeys and apes diverged, and these apes then underwent an adaptive radiation into 80 to 100 species. To put this number in context, there are only approximately 20 to 25 species of extant apes.

Morphological Features of Miocene Primates

How do we distinguish Miocene apes from contemporaneous monkeys? Although many morphological features are associated with apes, we focus on just a few key ones (Table 5.2). As you can see, most of the diagnostic features represent relative rather than absolute differences between the taxa. The overall set of character traits represents a more derived suite of features compared to monkeys. However, paleoanthropologists have failed to reach any consensus on a taxonomic classification for Miocene apes; each researcher favours sometimes radically different ideas. Because of this issue and because of the diversity of fossil apes during this time period, we'll split our review into three sequential sub-epochs: early, late, and middle Miocene.

Early Miocene Apes The early Miocene lasted from about 23 to 16 MYA. During this time, ape-like primates evolved in eastern Africa. Of the many species that have been found, the best, most abundant specimens are in the family Proconsulidae and genus *Proconsul.* These diurnal apes weighed from 17 to 50 kg, marking a major increase in body size within the primate clade. Despite this increase in body size, estimates of Proconsulidae brain size do not differ from those seen in Miocene monkeys. *Proconsul* had sexually dimorphic canines and a largely frugivorous diet (Figure 5.12). Most Proconsulidae were quadrupeds, although some species were more arboreal than others. Overall, *Proconsul* exhibits a mixture of both ape-like and monkey-like

TABLE 5.2

MAIN MORPHOLOGICAL DIFFERENCES BETWEEN MIOCENE AND EXTANT APES

Feature	Miocene Apes	Extant Apes
Placement of scapula	Side	Back
Rib-cage depth (front to back)	Deep	Shallow
Extension of elbow joint	Partial	Full
Shoulder joint	Restricted	Mobile
Spine	Long, flexible	Short, rigid
Hip joint	Restricted	Mobile
Arm to leg length	Equal	Arms longer
Hands	Small	Large

From Begun, 2003.

Formatter: Pls fix the line under "Extant Apes" traits. For example, these Miocene primates have the following ape-like features: relatively large body size, thick molar enamel, and no tail. However, *Proconsul* species retain some monkey-like features, such as certain morphological aspects of their backbone and pelvis. Other ape-like fossils, such as *Afropithecus* and *Kenyapithecus,* from the early Miocene also exhibit a variety of ape-like, monkey-like, and unique features. Thus, these early Miocene apes were probably better suited to travelling on top of tree branches rather than hanging or swinging below tree limbs, as seen in extant apes. Nonetheless, these cranial and postcranial features in early Miocene apes provide strong evidence for transitional changes in primate evolution.

Middle Miocene Apes During the middle Miocene (16.0–11.6 MYA), African apes moved across land bridges to colonize Eurasia and eventually parts of eastern Europe and Asia. Furthermore, David Begun (2003) hypothesizes that in the early stages of the middle Miocene epoch some European apes migrated back to Africa. However, these African immigrants did not last long, as most species appear to have gone extinct by about 13 MYA. Some of the best known and most interesting apes from middle Miocene are *Dryopithecus* from Europe and *Sivapithecus* from modern-day India and Pakistan. These primates were large, with body mass estimates of 20 to 90 kg. Just as in extant apes, *Dryopithecus* and *Sivapithecus* had teeth suited for masticating fruit pulp, shortened snouts, and long, strongly built jaws. A reduced snout represents a derived primate feature reflecting a reduced reliance on olfaction. The cranium of *Sivapithecus* is very similar to that of extant orangutans, although the postcrania of these two taxa have little in common. *Dryopithecus* brains were similar in size and proportions to those seen in extant chimpanzees, which are remarkably clever! Morphological interpretations of *Dryopithecus* and *Sivapithecus* postcrania reveal strong affinities to the suspensory locomotion utilized by extant apes. In sum, *Dryopithecus* and *Sivapithecus* were more ape-like than monkey-like.

Figure 5.12

Reconstructed skull from *Proconsul africanus*. © S. M. Lehman

Late Miocene Apes The late Miocene epoch lasted from 11.6 to 5.3 MYA, and experienced a continuous, gradual decline in global temperatures. In many regions of the world, temperate and tropical forests contracted in size due to reduced rainfall and temperatures. Although these changes likely resulted in the extinction of many ape taxa in Europe and parts of Asia, other taxa travelled to or continued to exist in the tropical zones of Africa and Southeast Asia. Consequently, some fossil apes, such as *Dryopithecus* and *Sivapithecus,* from the middle Miocene survived into the late Miocene. In addition, paleoanthropologists have recovered remains of some latecomers to the ape lineage, such as *Oreopithecus, Ouranopithecus, Lufengpithecus,* and *Ankarapithecus. Oreopithecus* is perhaps the best known of all the Miocene apes due to the abundant fossils discovered in Italy. This ape had the classic catarrhine dental formula of 2.1.2.3., and its dental morphology indicates a folivorous diet, which is a rather remarkable adaptation in the ape lineage. Most extant apes, except for some species of gorilla, are more frugivorous than folivorous. Although the body mass for *Oreopithecus* is estimated to be approximately 30 kg, which is rather large, this primate had a small brain, which is not an ape-like trait. Examination of the numerous postcranial remains for *Oreopithecus* indicates suspensory locomotion, just like in modern apes. *Ouranopithecus* was a large-bodied ape (70–110 kg) from what is modern-day Greece. This ape likely had a diet of hard, gritty foods. Like *Sivapithecus*, the face of *Ouranopithecus* is similar to that seen in modern orangutans. No postcranial materials have been recovered. *Lufengpithecus* was another large ape (50 kg), but from parts of southern China. These apes had extreme sexual dimorphism in their dentition and cranial features, which are similar to those seen in *Dryopithecus* specimens. You're probably just about ready to scream if you read about even one more *-pithecus*; but hold on, we have to consider only one more fascinating ape from the late Miocene. *Ankarapithecus* was a large-bodied (82 kg) ape from what is modern-day Turkey, and had teeth with very thick enamel and large jaws with which it likely masticated hard or gritty foods. *Ankarapithecus* retained the primitive trait of a **prognathic** face, which differs markedly from the flatter, more derived face of *Sivapithecus*. Now we can turn to the few monkeys known from the Miocene.

Prognathic ■ A forward or projecting aspect of anatomy, typically referring to the face.

Miocene Monkeys Although there were plenty of apes running around during the Miocene, this epoch seems to have supported few monkeys. Of the fossil monkeys that have been found, most have been recovered from the early to middle Miocene deposits in Africa and some isolated sites in Eurasia. Very few fossil monkeys have been found from the late Miocene. The reasons for this temporal variation in the fossil monkey assemblage are unknown at this time. What we do know is that the earliest Old World monkeys belong to a unique primate family called the Victoriapithecidae. Victoriapithecids ranged in body mass from 7 to 25 kg. They exhibit an interesting mixture of dental features, being more primitive than those seen in extant Old World monkeys yet more derived than those observed in Oligocene monkeys. For example, victoriapithecids have bilophodont molars with low molar cusps, as in cercopithecines. However, their mandibular morphology differs from that seen in earlier fossil monkeys and extant cercopithecines. Their postcranial morphology provides tantalizing evidence for partial terrestriality, which is not typically associated with the primitive arboreal lifestyle of fossil monkeys. The consensus of many paleoanthropologists is that victoriapithecids represent a mosaic of primitive and derived features indicative of a clade that eventually evolved into colobines and cercopithecines.

Phylogenetic Relationships among Miocene Primates

Each paleoanthropologist has his or her own slightly differing view on phylogenetic relationships within Miocene apes. Moreover, each researcher has formulated different hypotheses on which Miocene ape(s) evolved into living apes, like gorillas and chimpanzees. In most cases, these issues result from researcher speciality in one biogeographic region (e.g., Africa vs. Europe). We're only going to cover the "within" aspect of phylogenetics in fossil apes—in other words, we're not going to look at phylogenetic relationships between fossil and modern apes—as there is only tenuous evidence for relationships between fossil apes and extant apes. Many researchers group the small-bodied forms into the catarrhine monkey clade and the large-bodied taxa into the hominoid clade. You should note, again, that this over-reliance on one phenetic feature, body size, is not a particularly strong scientific method. Using a strict cladistic analysis of the total evidence, David Begun (2002) provides an interesting theory on the evolutionary history of Miocene apes (Figure 5.13). This theory holds that over the course of millions of years there were waves of migrations by Miocene apes out of and then back into Africa. In the early Miocene, fossil apes originated with *Proconsul* and then *Afropithecus* in Africa and the Arabian Peninsula. More derived forms then evolved during the middle to late Miocene in Africa (*Kenyapithecus*) and Europe (*Oreopithecus*). During the middle to late Miocene, two clades of Miocene apes existed in Europe (*Ouranopithecus* and *Dryopithecus*) and across a wide area of Eurasia (*Ankarapithecus*) and Asia (*Sivapithecus*, *Lufengpithecus*, *Sivapithecus*). Finally, the victoriapithecids tend to be positioned as basal to all extant Old World monkeys.

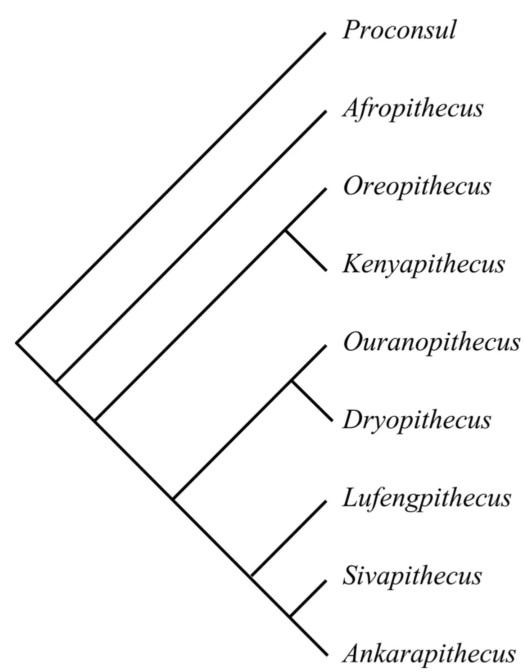

Figure 5.13

Phylogenetic relationships of Miocene primates.

Pliocene Primates: Return of the Monkeys!

The Pliocene epoch lasted from 5.3 MYA to approximately 1.8 MYA. During this epoch, a land connection formed between North and South America via the Panama isthmus. The Tethys Sea became isolated and eventually formed part of what is now the Mediterranean Sea. Due in part to the formation of continental land bridges and isolated seas, the climate continued to be cool and dry over the course of the Pliocene, further reducing the size and expanse of tropical forests. Temperate regions continued to transition from forests to grasslands.

Morphological Features of Pliocene Primates

The above geographic and climate changes spelled the end of the "Age of the Apes" and heralded a broad radiation of monkeys and the earliest hominins, which we meet in Chapter 6. Pliocene monkeys have been unearthed in Africa, Europe, and Asia. In fact, some specimens have been recovered from southeastern Britain and the Island of Sicily, representing places you might not think of as former monkey habitats. These Pliocene primates are similar in many ways to extant cercopithecines and colobines, which are part of the Cercopithecidae family. Let's meet the cool Pliocene monkeys!

Fossil Cercopithecinae Fossil cercopithecines represent a diverse assemblage of primates from Africa and Asia. Of the 10 genera of Pliocene cercopithecines described to date, 5 still exist (*Macaca, Papio, Cercocebus, Theropithecus,* and *Cercopithecus*), indicating the success of this radiation to last for millions of years. Body mass estimates for these monkeys range from 9.5 kg in the relatively small-bodied *Macaca* up to the so-called giant geladas, which weighed about 96 kg (Figure 5.14)! Modern geladas weigh only 11 to 19 kg. Given the diversity of fossil cercopithecines, it is beyond the scope of this book to summarize all their interesting dental and postcranial morphologies. What we can say here about these fossil primates is that they share a suite of dental, cranial, and postcranial features similar to those seen in extant macaques; mangabeys, baboons, and geladas; and guenons. Consequently, their diet and locomotor behaviour are likely similar to those seen in extant congenera.

Fossil Colobinae Fossil colobines have been unearthed in many of the same regions as those that produced fossil cercopithecines (i.e., Europe, Asia, and Africa). Paleoanthropologists have described approximately 12 genera of fossil colobines from the Pliocene. These Pliocene monkeys ranged in body mass from 4 to 35 kg. Although some fossil and extant colobines share morphological similarities, many fossil colobines look remarkably different from extant members of this subfamily. Specifically, many of the fossil colobines retain primitive Cercopithecidae characteristics of low molars cusps, compared to high molar cusps used for shearing leafy materials in extant colobines, and postcranial evidence for terrestriality. Extant colobines are almost exclusively arboreal. Moreover, some fossil colobines were much larger in body size than extant taxa in this subfamily. The largest living colobine weighs about 11 kg.

Phylogenetic Relationships among Pliocene Monkeys

The phylogenetic relationships among Pliocene monkeys are, for lack of a more scientific word, a mess: particularly for the colobines. Part of this phylogenetic issue results from the fact that we define extant cercopithecines and colobines by certain aspects of soft tissues, such as cheek pouches and stomach anatomy. It is extremely rare for any soft tissue to fossilize, and that which does is usually skin and hair rather than any internal structures. The incomplete fossil record for many Pliocene monkeys also contributes to heated debates about their phylogenetic relationships. There are as many morphological similarities between fossil and extant cercopithecines as there are morphological differences between fossil and living colobines. Therefore, given that we cannot resolve evolutionary relationships between these basal monkeys, a complete review of the phylogenetic relationships to extant monkeys is best left for more advanced work and study. Despite these issues, there is no valid scientific reason to invoke either intelligent design or creationism as alternatives to evolution when reviewing Pliocene monkeys (Figure 5.15). As more fossil primates are recovered and new phylogenetic techniques are employed, researchers will be better prepared to resolve phylogenetic relationships in Pliocene monkeys.

Summary

1. Fossil primates are represented largely by dental remains; cranial and postcranial materials are rarely found. Thus, most research on primate origins involves detailed analysis of teeth.
2. General patterns of diet, locomotion, activity patterns, and even social organization can be learned from careful studies of fossil primates. Specifically, paleoanthropologists use the comparative method to understand morphological adaptations in fossil primates.
3. There are three main hypotheses on primate origins: the arboreal theory, the visual predation theory, and the angiosperm co-evolution theory.
4. The earliest mammals somehow survived a massive global extinction event about 65 million years ago. It is possible that the first primates evolved before or during the Paleocene, although the first definitive primates show up in the Eocene. Oligocene primates exhibit broad morphological similarities to some modern monkeys. The Miocene witnessed an explosive radiation of ape-like primates, which slowly disappeared during the Pliocene.

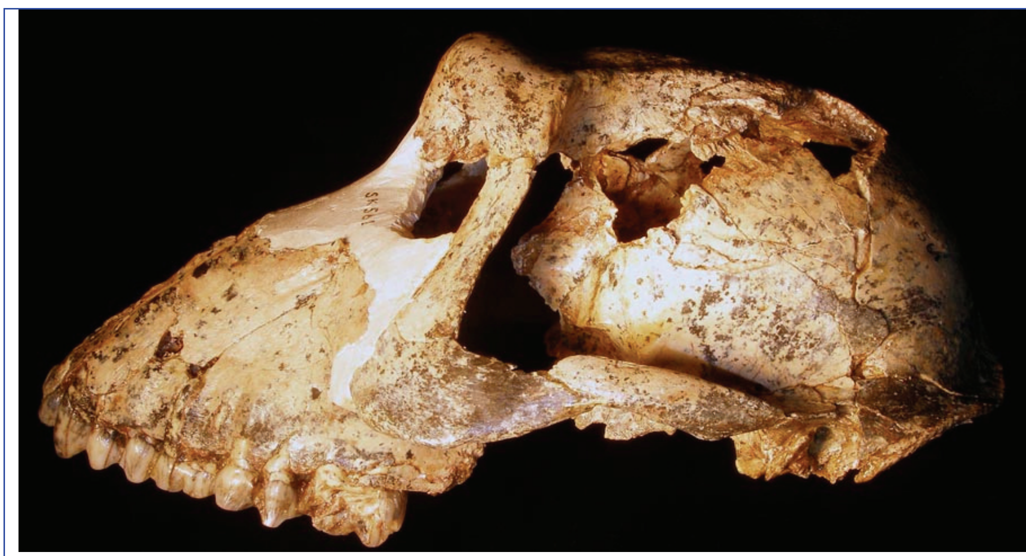

Figure 5.14

Side view of skull from *Theropithecus oswaldi.*

This was a giant, extinct cercopithecine that lived during the Pliocene.

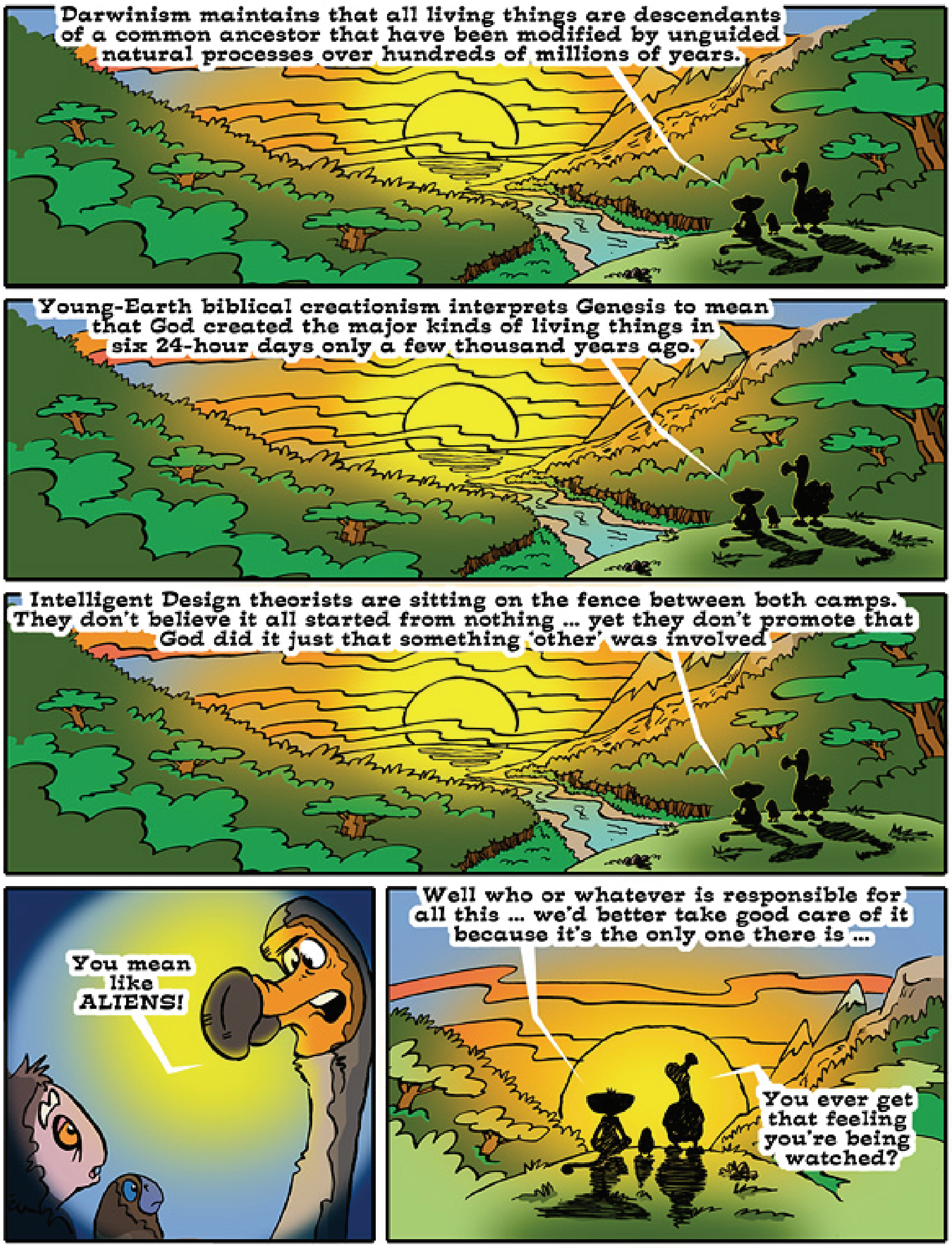

Figure 5.15

Just because evolutionary anthropologists are unable to answer every question on primate and human origins does not mean that there is any support for creationism or intelligent design.

INTERNET RESOURCES

PALEOMAP Project
www.scotese.com
See some cool geological maps and climatic models for the Cenozoic.

Dental Microwear
http://comp.uark.edu/~pungar
Learn about reconstructing the diet of fossil primate and hominins.

eSkeletons Project
www.eskeletons.org
See and compare primate dental, cranial, and postcranial morphologies.

Duke University Lemur Center
www.fossils.duke.edu/learn/BAA246/BAA246.html
See photos and learn about fossil primates at the Division of Fossil Primates of this Duke University Lemur Center site.

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