

9.5 Apes Begin in Africa and Dominate the Miocene Primate World

After the Oligocene, the strength and completeness of the higher primate fossil record derives from rich Miocene geologic deposits in East Africa, especially in the present-day countries of Kenya and Uganda (**Figure 9.18**). Just before this time, a warming trend in the Late Oligocene provided the conditions for a shift in habitats and the appearance of a new and widespread radiation of a group of catarrhine primates called the **proconsulids**, mostly dating to roughly 22–17 mya (**Figure 9.19**). Recall that the last of the Oligocene primate fossils, in Egypt and Saudi Arabia, date to about 29–28 mya. This means that about a 6-million-year gap exists between the Late Oligocene catarrhines (28 mya) and the first Miocene proconsulids (22 mya). As a consequence, the immediate ancestors of proconsulids are a mystery. However, the strong anatomical similarity in skulls and in teeth between Oligocene catarrhines from the Fayum and the Arabian Peninsula and the proconsulids of the Miocene indicates a likely ancestral–descendant relationship between the earlier and later groups. For example, all of these primates have a dental formula of

groups. For example, all of these primates have a dental formula of $2/1/2/3$, and their upper incisors are broad and flat.

The proconsulids are represented by a diversity of taxa—as many as 10 genera and 15 species—from the Early and Middle Miocene. In fact, the diversity of the extinct apes in the Miocene is much greater than that of living apes today. For example, proconsulids ranged from the tiny *Micropithecus*, the size of a small New World monkey, to the namesake genus, *Proconsul*, a species of which, *Proconsul major*, was about the size of a modern male chimpanzee, weighing about 50 kg (110 lb). *Proconsul* is the best known of the Early to Middle Miocene apes from Africa, in part thanks to a nearly complete skeleton discovered on Rusinga Island, in western Kenya's Lake Victoria, in the late 1940s (Figure 9.20). Reflecting the proconsulids' biological diversity, their fossils have been found in a range of settings, representing different climates and environments, from open woodlands to tropics. Reflecting these different habitats, their diets varied considerably.

The skulls and teeth of the Miocene proconsulids were clearly like those of apes in overall appearance. The molars have the Y-5 pattern, and the cusps are wide and rounded for eating fruit. There are well-developed honing surfaces on the backs of the upper canines and the fronts of the lower third premolars. Comparisons of tooth wear in living apes and in extinct Miocene apes suggest that some of the extinct apes ate leaves and some ate nuts and fruit, but that most of them routinely ate ripe fruit.

In contrast to the skulls and teeth, the rest of the

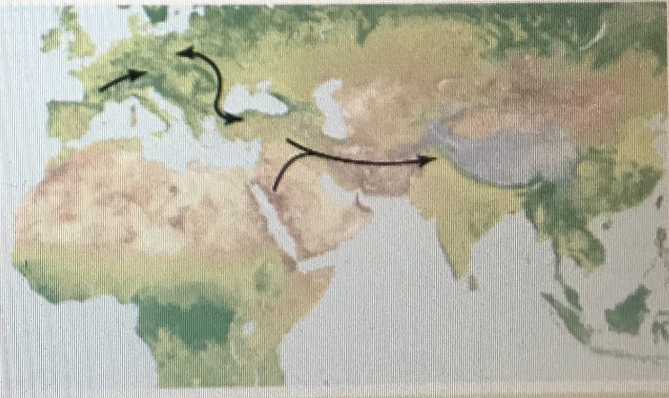


In contrast to the skulls and teeth, the rest of the skeleton of Miocene apes is generally like that of monkeys (Figure 9.21). Unlike the living apes, these primitive apes had front and hind limbs that were equally long and that lacked specializations for knuckle-walking or arm-swinging that we see in today's apes. Moreover, like Old World monkeys, *Proconsul* had wrist bones (carpals) that articulated directly with the ulna, one of the two forearm bones. This direct articulation, a primitive characteristic, indicates relatively limited wrist mobility, whereas living apes have highly mobile wrists for arm-swinging and arm-hanging. Proconsulids' elbows could straighten only so far, whereas living apes' elbows can extend completely. Proconsulids' feet combined primitive and derived features—some of the anklebones were slender, like monkeys', but the big toes were large, like apes'. The

whole package suggests that *Proconsul*, unlike living apes, walked on the tops of tree branches on all fours. Because these creatures lacked a number of anatomical features that living hominoids share, they can be used as a model of the animals that gave rise to the last common ancestor of all later hominoids.



1 Out of Africa to Europe (17-16.5 mya)



2 Spread throughout Europe and Asia (16-14 mya)

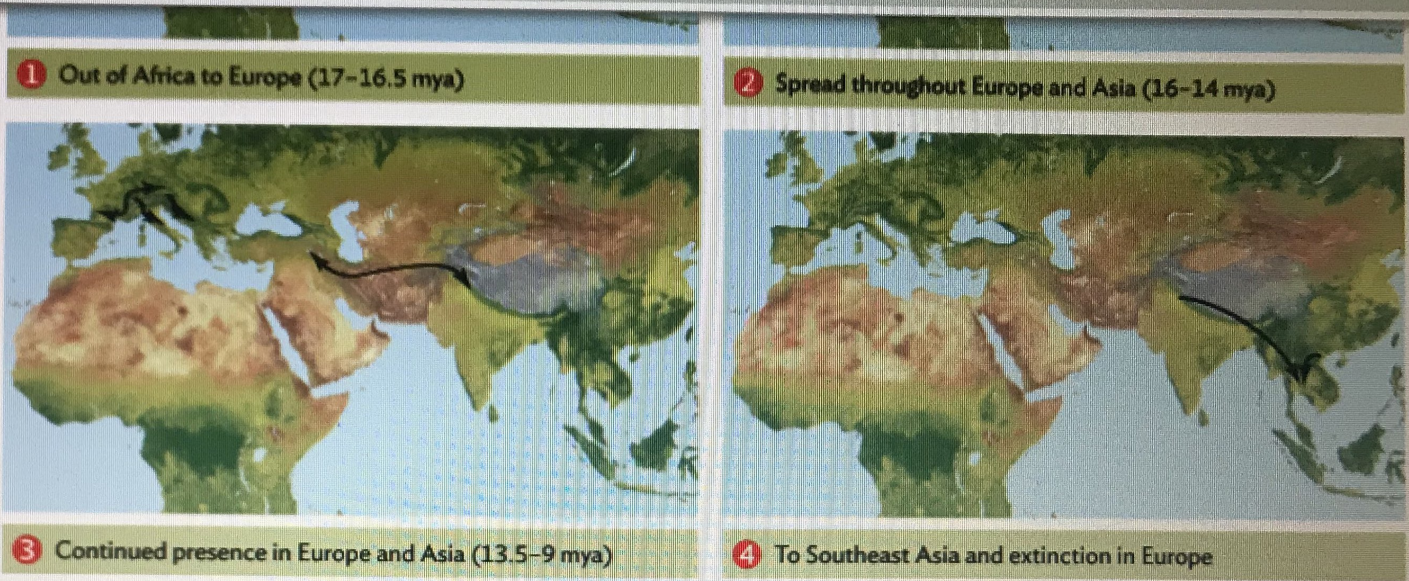


FIGURE 9.18

Miocene Ape Fossil Localities A wide variety of ape fossils have been found in Miocene deposits in Africa, Asia, and Europe. These fossils provide a record of evolution and location during this dynamic period of hominoid evolution. The first proconsulids—*Proconsul*, *Afropithecus*, and *Kenyapithecus*—arose in East Africa. During the next 10–11 million years, these and related apes migrated from Africa to Europe and western Asia (map 1), diversified in Europe and western Asia (map 2), a process that continued in Europe and western Asia (map 3), and eventually into eastern Asia (map 4).

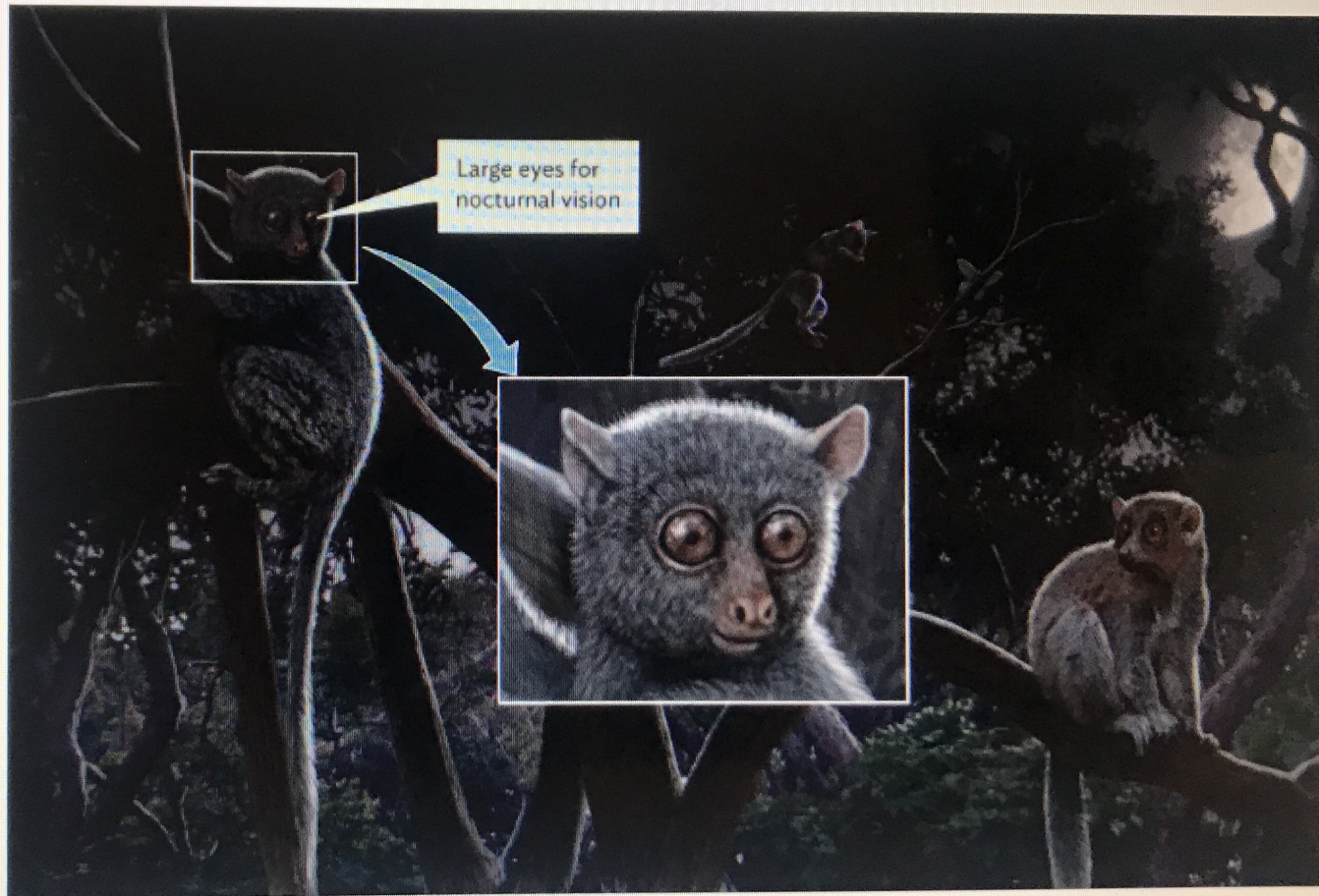
9.19

Eocene–Oligocene–Miocene Habitats and Their Primates



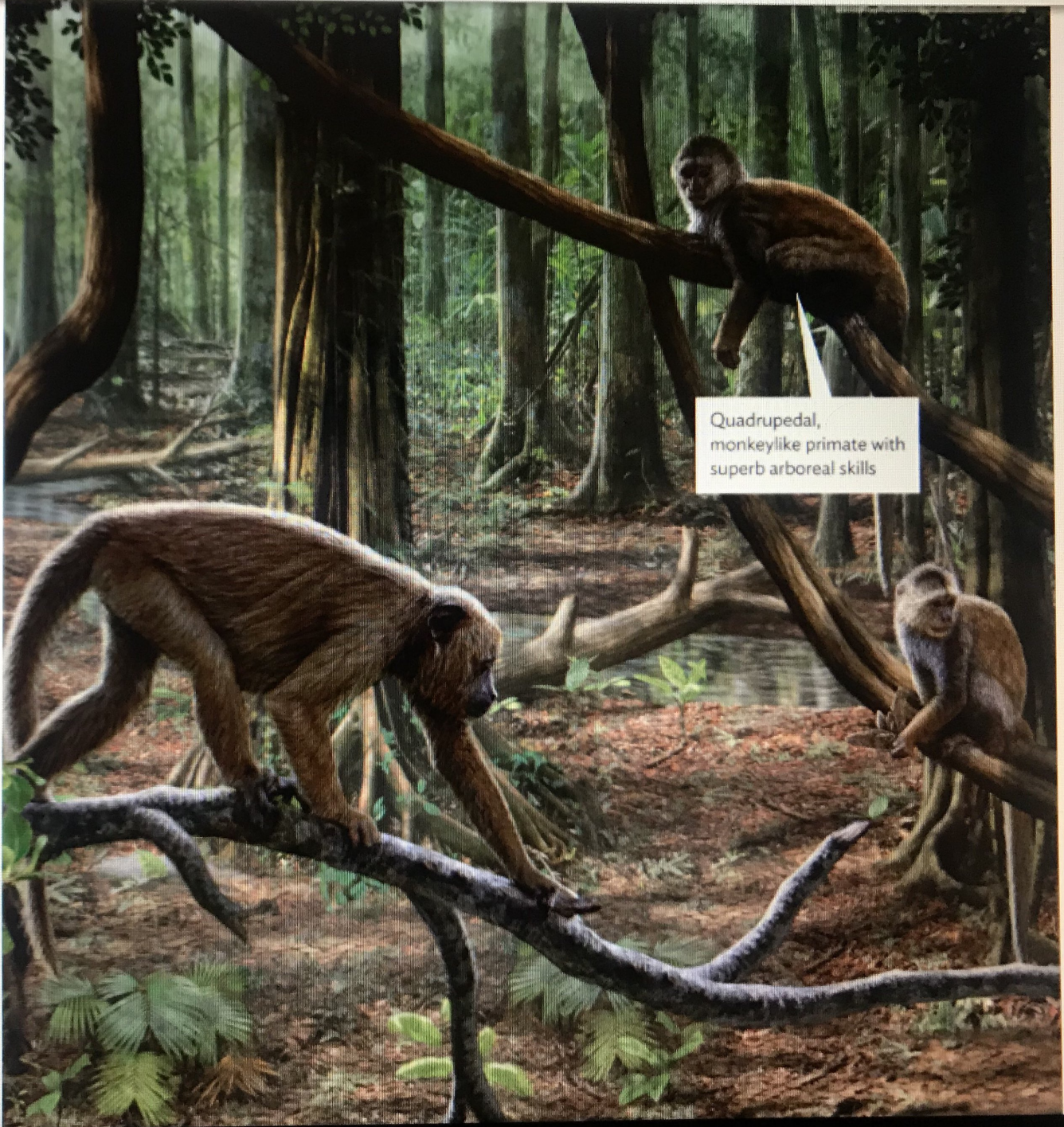
Primate evolution began with primitive primates in the Eocene, setting the stage for the origin of all hominoids. Euprimates of the Eocene had the basic characteristics of living primates, such as

all hominoids. Euprimates of the Eocene had the basic characteristics of living primates, such as convergent eye orbits and grasping digits. In the past 20 million years, primates diversified in appearance and behavior. These changes included the shift, for some, from life in the trees to life on the ground, and eventually the beginning of bipedalism in the late Miocene. (Based on Fleagle, J. G. *Primate Adaptation and Evolution*, 2nd ed. 1999. Academic Press.)

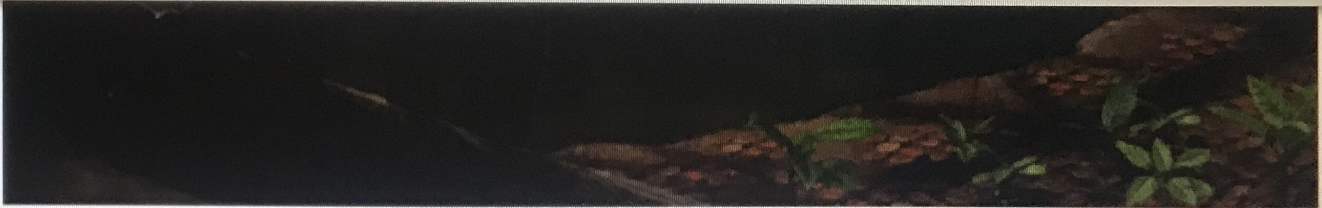


Scenes from the late Eocene in the Paris Basin. **Top:** The diurnal *Adapis* is feeding on leaves. **Bottom:** Several taxa of omomyids (*Pseudoloris*, *Necrolemur*, *Microchoerus*). Note the large eyes, a nocturnal adaptation, typical of both ancient and modern prosimians who are active at night.

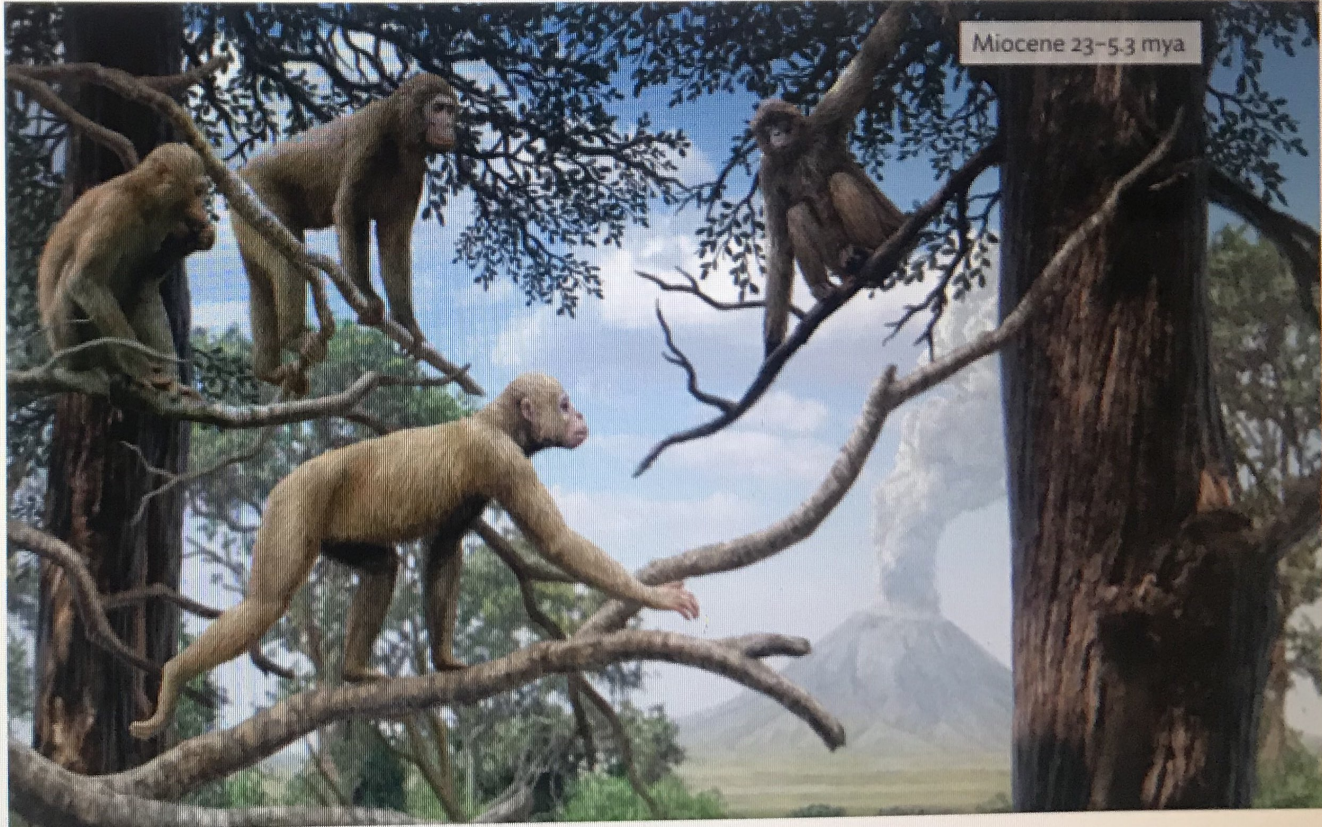


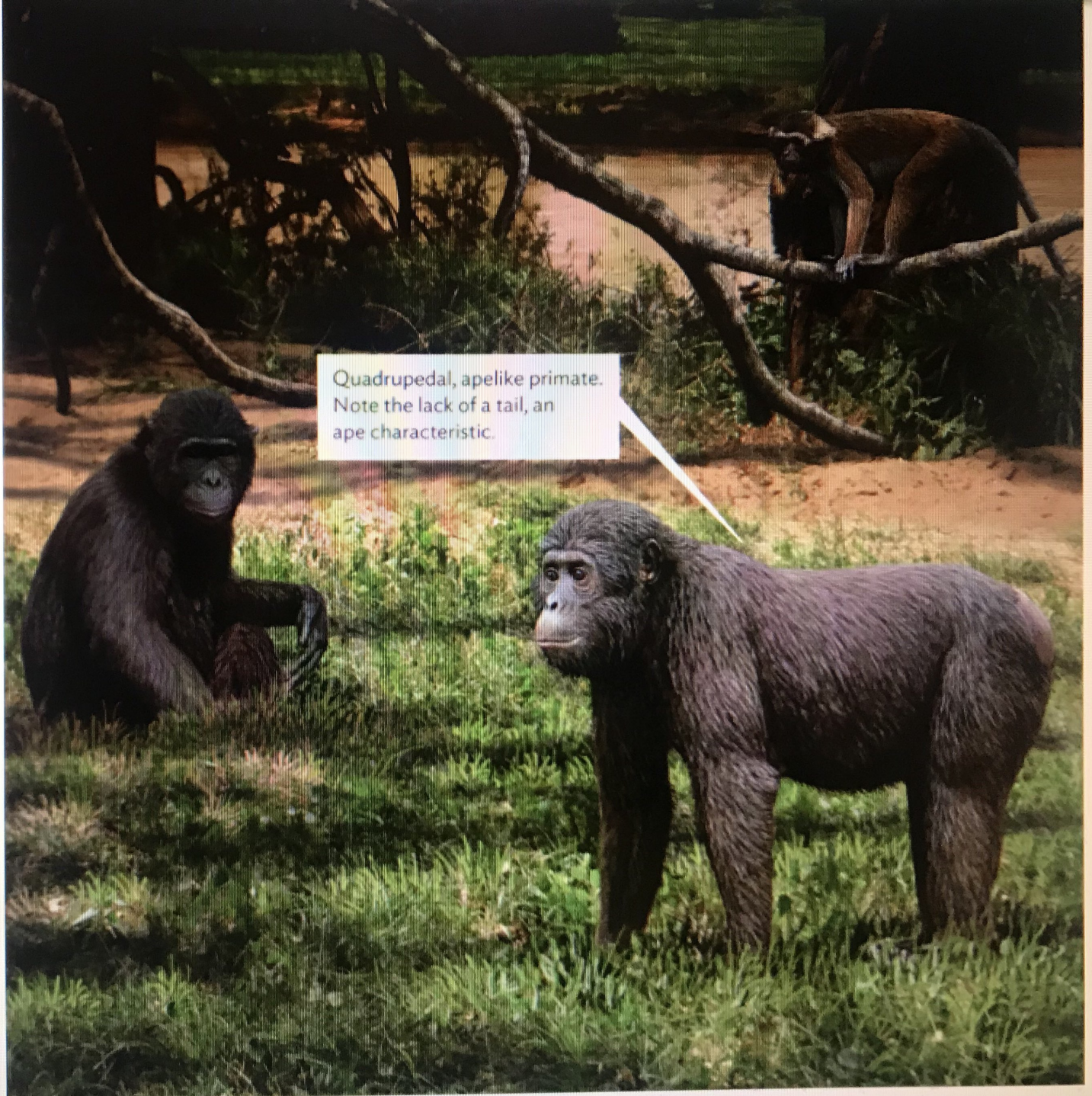


Quadrupedal,
monkeylike primate with
superb arboreal skills



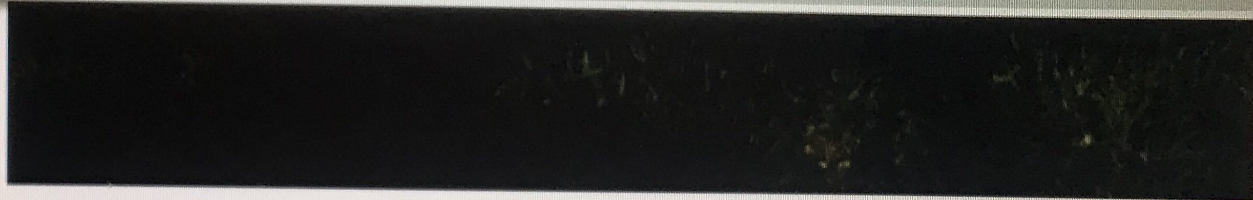
Scenes from the early Oligocene of the Fayum, Egypt. These anthropoid ancestors include *Aegyptopithecus*, *Propliopithecus*, and *Apidium*. These primates were adept arborealists, using their hands and feet for climbing and feeding.





Quadrupedal, apelike primate.
Note the lack of a tail, an
ape characteristic.

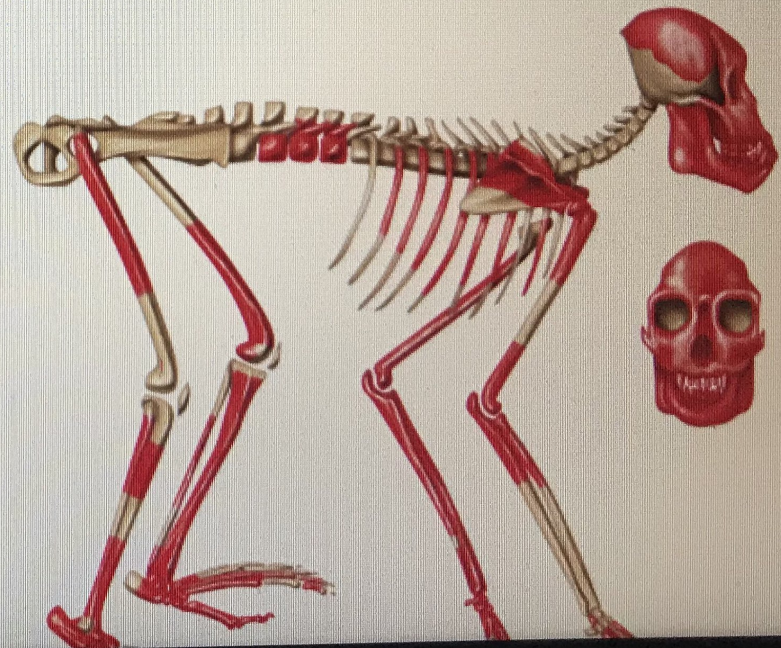
Scene from the early Miocene of Rusinga Island, Kenya. Apes first appeared during this period, and



Scene from the early Miocene of Rusinga Island, Kenya. Apes first appeared during this period, and these are the first apes (two species of *Proconsul*, *Dendropithecus*, *Limnopithecus*). These and other taxa form the ancestry of all later apes and hominins. Note the range of habitats occupied by these primates within the forest, including some in the middle and lower canopies and some on the forest floor. These primates show a combination of monkeylike and apelike features, in the skeleton and skull, respectively.



(a)





(a)



(c)



(b)

FIGURE 9.20

Proconsul This Miocene ape genus was first found in Kenya in 1909—it was the first fossil mammal ever discovered in that region of Africa. *Proconsul* literally means “before Consul”; *Consul* was the name given to chimpanzees that performed in European circuses. *Proconsul*, then, is considered an ancestor to apes, including chimpanzees. (a) The first skull of the genus was found in 1948 and was nearly complete. The cranial remains helped researchers determine that *Proconsul* was possibly an ancestor to apes. (b) Other fossil finds have helped researchers determine what *Proconsul*'s full skeleton was like. Note that it lacked a tail, like all modern apes. Here, areas shaded red represent the parts of the skeleton that have been discovered. (c) An artist's reconstruction illustrates *Proconsul*'s rainforest habitat and arboreal nature. (Figure 9.20c: “*Proconsul heseloni* Habitation,” © 1992 by Jay H. Matternes)