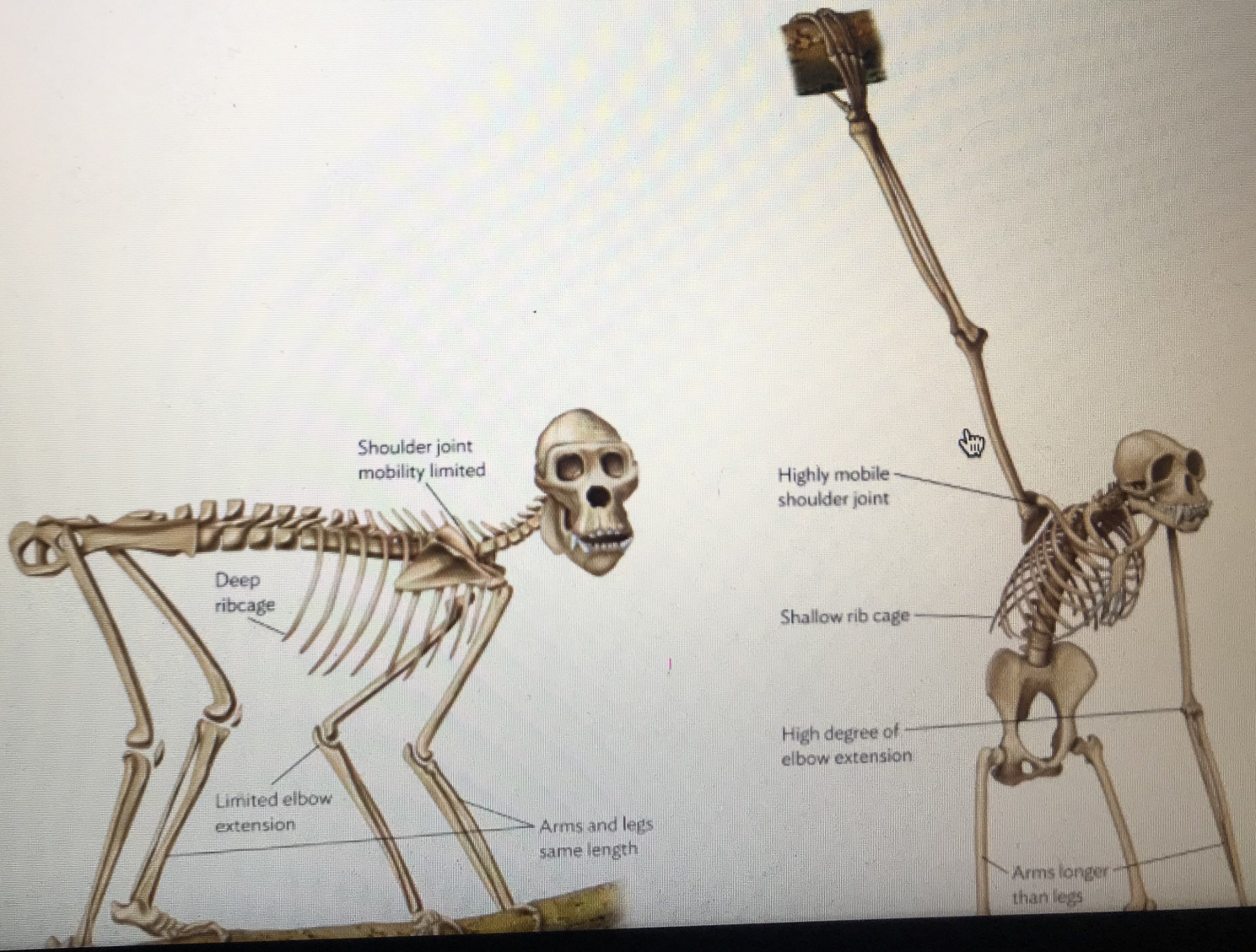
9.6 Apes Leave Africa: On to New Habitats and New Adaptations

The presence of ape fossils in Europe and Asia from about 17 mya (but not before) suggests that apes originated in Africa and then spread to Europe and Asia. The migration of primates (and other animals) from Africa to Europe and Asia was made possible by a land bridge created 23–18 mya by a drop in sea levels and the joining of the African–Arabian tectonic plate with Eurasia. After their dispersal into Europe and Asia, apes became more diverse than ever before, thus representing an extraordinary adaptive radiation, among the most successful among higher primates.

Apes in Europe: The Dryopithecids

By 13 mya, the early apes had successfully adapted to a wide range of new habitats. During this time, Europe was covered by a dense, subtropical forest that provided a rich variety of foods, especially fruit. *Dryopithecus*, the best-known genus within a group of great apes called dryopithecids, lived in the area of Europe that is now the countries of France and Spain. Larger than earlier apes—about the size of a chimpanzee—it was first discovered and described by the eminent

France and Spain. Larger than earlier apes—about the size of a chimpanzee—it was first discovered and described by the eminent French paleontologist Edward Lartet (1801–1871) in 1856 in St. Gaudens, southern France. *Dryopithecus* and its contemporary taxa are known from other European regions, such as Spain, Greece, and Hungary.



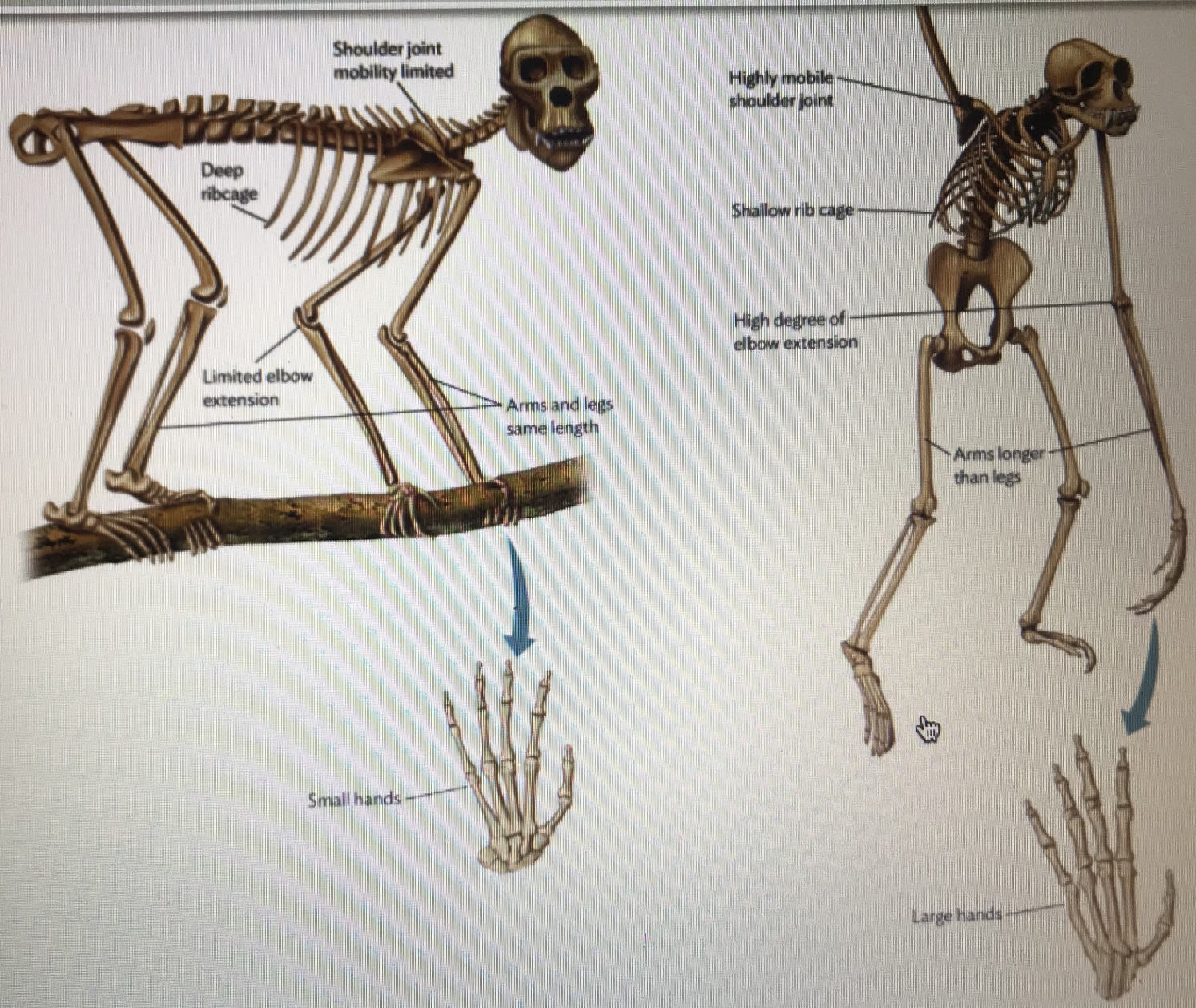
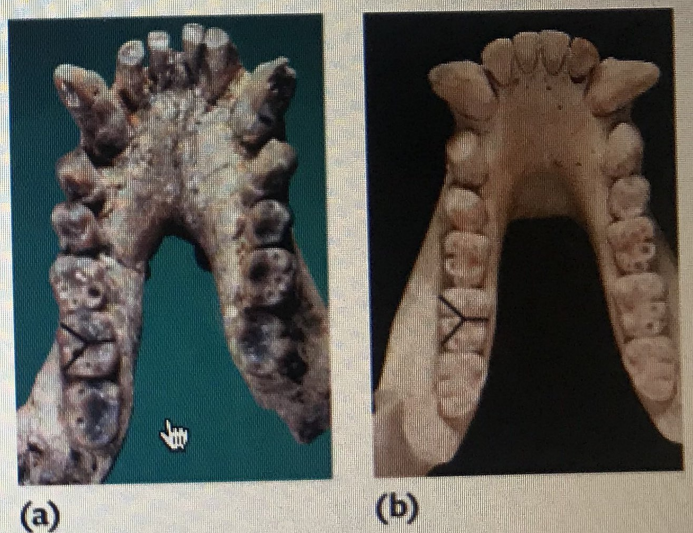


FIGURE 9.21
Proconsulid Body Plan The body plan of primitive, Miocene apes (left) differs from that of modern apes (right). The Miocene apes had a more monkeylike body, with smaller hands, a more restricted hip joint, and a more flexible spine. Modern apes have highly mobile shoulder joints and fully extendable elbow

FIGURE 9.21
Proconsulid Body Plan The body plan of primitive, Miocene apes (left) differs from that of modern apes (right). The Miocene apes had a more monkeylike body, with smaller hands, a more restricted hip joint, and a more flexible spine. Modern apes have highly mobile shoulder joints and fully extendable elbow joints, enabling them to brachiate, or swing from branch to branch; the Miocene apes, by contrast, probably were arboreal quadrupeds, not needing the great mobility in their shoulders and their wrists. For the purposes of comparison, this Miocene ape, *Proconsul*, and this lesser ape, the modern gibbon, have been drawn the same size. In reality, *Proconsul* was about half the size of a gibbon.

Dryopithecus resembled living apes in many ways: its canines were sharp and tusklike; its cheek teeth were long and had very simple chewing surfaces, well-adapted for chewing fruit (**Figure 9.22**); and microscopic studies of cross sections of the teeth enamel indicate that these apes grew slowly. Their brains were larger than those of earlier primates, similar to those of modern chimpanzees. Their long forelimbs, grasping feet, and long, grasping hands were powerful and adapted for arm-hanging and arm-swinging, modern apes' main forms of locomotion.



(a) (b)

FIGURE 9.22
Dryopithecus (a) The mandible of *Dryopithecus*, a Miocene ape genus from Europe, like that of **(b)** a modern gorilla, includes the Y-5 molar pattern and low, rounded cusps. Both also have large canines, plus the diastema between the canine and the first premolar.

Apes in Asia: The Sivapithecids

In Asia, the sivapithecids were the counterpart of Europe's dryopithecids. The best-known sivapithecid is *Sivapithecus*,

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Apes in Asia: The Sivapithecids

In Asia, the **sivapithecids** were the counterpart of Europe's dryopithecids. The best-known sivapithecid is ***Sivapithecus***, an ape ancestor that thrived about 12–8 mya. Whereas chimpanzees and gorillas have thin-enameled teeth, *Sivapithecus* had thick-enameled teeth, adapted for eating hard, tough-textured foods such as seeds and nuts. Its robust jawbones were similarly adapted.

Because hominins also have thick-enameled teeth, primatologists once thought *Sivapithecus* was the ancestor of hominins. This hypothesis was rejected in 1979, when the anthropologists David Pilbeam and Ibrahim Shah discovered a partial *Sivapithecus* skull (**Figure 9.23**). *Sivapithecus* skulls are strikingly similar to those of living orangutans, with concave faces, narrow nasal bones, oval eye orbits from top to bottom, projecting premaxillas (the *premaxilla* is the area of the face below the nose), large upper central incisors, and tiny lateral incisors. Even more similar to living orangutans, however, is the newly discovered ***Khoratpithecus***, a hominoid of the Late Miocene (9–6 mya) in Thailand. Various features of this primate's teeth and lower jaw—for example, broad front teeth, and canines with a flat surface on the tongue side—indicate that this Miocene primate is living orangutans' most likely ancestor.

Closely related to *Sivapithecus*, *Khoratpithecus*, and other Asian Miocene apes is a very interesting pongid, ***Gigantopithecus***, from India, northern Vietnam, and southern China, dating to about 8–0.3 mya (**Figure 9.24**). Appropriately named for its massive body,

northern Vietnam, and southern China, dating to about 8–0.3 mya (**Figure 9.24**). Appropriately named for its massive body, *Gigantopithecus* is the biggest primate that has ever lived, standing nearly 3 m (10 ft) tall and weighing as much as 300 kg (660 lb)! Its massiveness would have limited this fossil primate to the ground for all its activities. Like some of the other Miocene apes, it had thick-enameled teeth and large, thick-boned jaws, adapted for eating very hard foods, likely nuts, seeds, fruits, leaves, and stems.

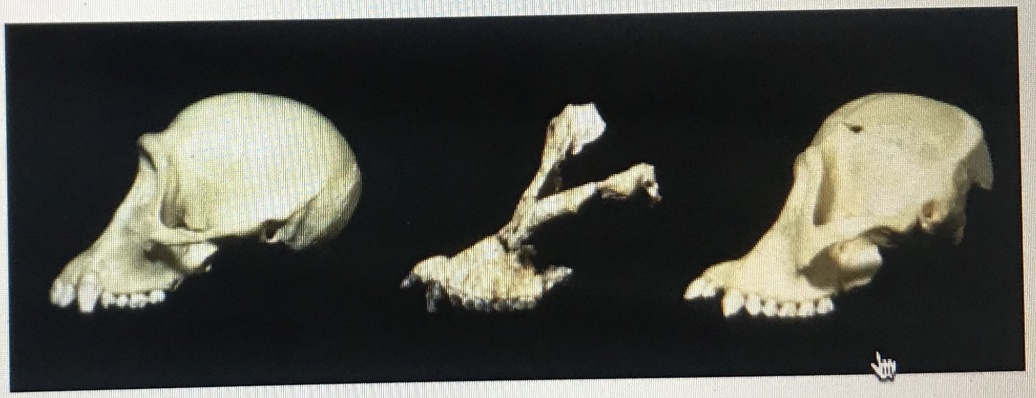

FIGURE 9.23
Sivapithecus Originally found in the Siwalik Hills of modern-day India and Pakistan, this Miocene ape (center) has been proposed as ancestral to the orangutan (right). *Sivapithecus*'s facial features, for example, are far closer to the orangutan's than to those of other great apes, such as the chimpanzee (left). *Sivapithecus* has three species, any of which may be a direct ancestor to the orangutan; however, recent finds of another Miocene ape genus have called this ancestry into question.

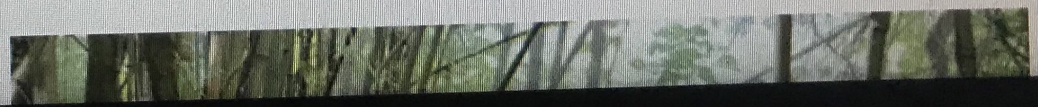

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FIGURE 9.24
Gigantopithecus Bamboo was probably among the plant foods eaten by this enormous, herbivorous Miocene ape. Climate change and competition with other primate species likely brought about this ape's extinction.


Tuscany
ITALY
Sardinia

Dead End in Ape Evolution: The Oreopithecids

Around the same time *Gigantopithecus* emerged, a group of apes called **oreopithecids** lived in Europe. They appear in the fossil record around 8 mya and disappear around 7 mya. ***Oreopithecus***, the best known of this group, has been found on the island of Sardinia and in coal mines in Tuscany, Italy. (Oreopithecids were also present in Africa at the same time as the proconsulids on that continent.) Its Miocene habitat was dense, tropical forests, and its teeth were highly specialized for eating leaves (**Figure 9.25**). Also known as the "Swamp Ape," *Oreopithecus* was a medium-size primate, weighing an estimated 30–35 kg (66–77 lb), but it had a tiny brain. Its relatively long arms indicate that it was adept at some form of suspensory locomotion, similar to that of a modern gibbon. Some of its hand adaptations foreshadow developments in hominin evolution.

FIGURE 9.25
Oreopithecus The high, shearing crests on its molars suggest that this Miocene ape was folivorous. Like *Gigantopithecus*, this ancestral ape likely became extinct due to climate change.

Climate Shifts and Habitat Changes

During the period in which *Oreopithecus* and other later Miocene apes disappeared, Europe, Asia, and Africa experienced dramatic changes

During the period in which *Oreopithecus* and other later Miocene apes disappeared, Europe, Asia, and Africa experienced dramatic changes in climate and ecology. Several factors coincided to cause these changes: a shift in tectonic plates created the Alps, the Himalayas, and the East African mountain chains; ocean currents shifted; and the polar ice caps began to re-form. In Europe and then Africa, the once-lush tropical forests changed to cooler, drier mixed woodlands and grasslands. As a result, tropical foods disappeared, including the apes' favored diet, fruit. In Asia, a decrease in rainfall, reduced forests, and decreased fruit availability likely contributed to the extinction of *Sivapithecus*.

CONCEPT CHECK

The First Apes: A Remarkable Radiation

The apes' evolutionary glory days were in the Miocene epoch (23–5.3 mya), beginning in Africa and then spreading into Europe and Asia. Out of this remarkable adaptive radiation came the ancestors of living apes and of humans. All of these fossil primates had characteristics seen in living apes, especially in the teeth and the skull (Y-5 lower molars, 2/1/2/3 dental formula, broad incisors, large honing canines), but most were monkeylike

the ancestors of living apes and of humans. All of these fossil primates had characteristics seen in living apes, especially in the teeth and the skull (Y-5 lower molars, 2/1/2/3 dental formula, broad incisors, large honing canines), but most were monkeylike in the postcranial skeleton (front and back limbs equally long).

Group	Characteristics	Age	Location
Proconsulids 	Large range in size Tropics to open woodlands Thin enamel (e.g., *Proconsul*)	22–17 mya	Africa (Kenya, Uganda)
Dryopithecids 	Some size range Tropics Thin enamel (e.g., *Dryopithecus*)	14–9 mya	Europe (France, Spain, Germany, Greece, elsewhere)
Sivapithecids 	Some size range Tropics Thick enamel Skull like orangutan's (e.g., *Sivapithecus*)	14–8 mya	Asia (Pakistan, India, China, Thailand)

	Tropics Thick enamel Skull like orangutan's (e.g., *Sivapithecus*)		(Pakistan, India, China, Thailand)
Oreopithecids 	Large body Tiny brain Specialized molars for eating leaves Suspensory locomotion (e.g., *Oreopithecus*)	9–7 mya	Europe (Italy), earlier form in East Africa (Kenya)

Miocene Ape Survivors Give Rise to Modern Apes

A handful of ape taxa survived these dramatic disruptions in habitat. *Khoratpithecus,* for example, thrived for a time and gave rise to the orangutan of Southeast Asia. The origins of the great apes of Africa and hominins are far less clear. In fact, only one small set of fossils—named *Chororapithecus* by their discoverer, the Japanese paleoanthropologist Gen Suwa—resembles similar parts of living great apes. Teeth representing three individuals, found in Ethiopia and dating to about 10.5 mya, are remarkably similar to the modern gorilla's teeth. Their existence suggests that Late Miocene African

	Suspensory locomotion (e.g., *Oreopithecus*)		East Africa (Kenya)

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9.7 Apes Return to Africa?

Ape fossils from the Late Miocene might be so scarce in East Africa because apes simply were not living there, at least not in great numbers, at that time. Somewhere other than Africa may be the source of living African apes' and humans' common ancestor. The Canadian primate paleontologist David Begun suggests that Late Miocene Europe might yield that ancestor. He speculates that the similarities in dentition and skull between the Greek dryopithecid *Ouranopithecus*, on the one hand, and African apes and early hominins, on the other, indicate an ancestral–descendant relationship between European great apes and African hominins. Begun argues that the climate changes in Europe prompted Late Miocene apes to move from Europe back to Africa, essentially following the tropical forests, and the foods these forests provided, as forests and foods disappeared behind them. Some of the pongids adapted to forested settings, some lived in woodlands, and eventually one group, hominins, became committed to life on the ground. However, the record of hominoid evolution in Africa and the clear presence of the earliest hominins in Africa favors an African origin of today's apes and humans. Thus, it is likely that the European pongids went extinct in the late Miocene.