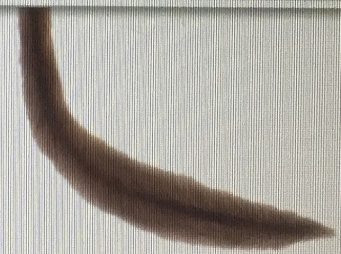


## 9.2 The First True Primate: Visual, Tree-Dwelling, Agile, Smart Primates in the Paleocene?

We know *generally when* the first primates appeared—almost certainly in the early Cenozoic era. But just how early in the Cenozoic is debated by the paleontologists who study early primate evolution. They have reached no consensus as to whether the first primates appeared in the Paleocene epoch, which began 66 mya, or in the following epoch, the Eocene, which began 56 mya. The Paleocene candidate for the first primates is a highly diverse, highly successful group of primitive mammals called the **plesiadapiforms**, which lived in western North America, western Europe, Asia, and possibly Africa. The oldest plesiadapiforms are from North America, indicating the possibility that the origins of order Primates is in the New World. These animals represent an adaptive radiation that flourished over a 10-million-year period, beginning at the start of the Paleocene.



**FIGURE 9.5**

**Plesiadapis** These primatelike mammals were an ancestral lineage leading to true primate ancestors. (a) As this *Plesiadapis* skull illustrates, plesiadapiforms did not possess primates' postorbital bar. And while primates have a versatile dentition, plesiadapiforms had very specialized anterior (front) teeth, which were separated from the posterior (rear) teeth by a large gap. In addition, *Plesiadapis* and other plesiadapiforms had much smaller brains than those of true primate ancestors. (b) This reconstruction of *Plesiadapis* reflects similarities to and differences from modern primates.

Despite their amazing diversity and geographic spread, by about 56 mya most of the plesiadapiforms had gone extinct. Were they primates? Perhaps not. The problem with attributing them to order Primates is that they lack the key characteristics that define primates today. That is, in contrast to primates, the plesiadapiforms lacked a postorbital bar and convergent eye orbits, their digits were not especially well adapted for grasping tree branches (they lacked opposability), their digits lacked nails (they had claws), their teeth were highly specialized (some even had three cusps on their upper incisors, as opposed to the single cusp of most primates today), and their brains were tiny (**Figure 9.5**). Moreover, some plesiadapiforms lacked the petrosal bulla, a part of the temporal bone that contains the middle-

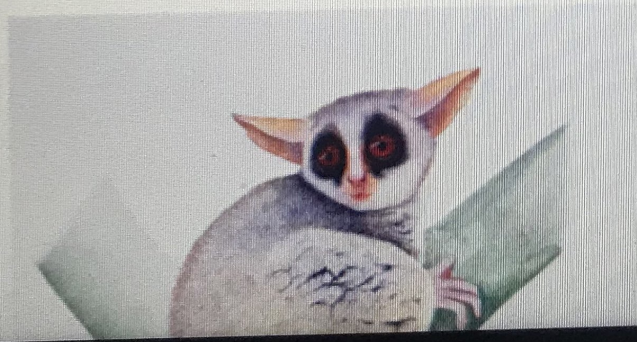
petrosal bulla, a part of the temporal bone that contains the middle-ear bones and is present in all primates. Because of their potential relationship with the first true primates, the American paleontologist Philip Gingerich has called them **Proprimates**, a separate order from Primates.

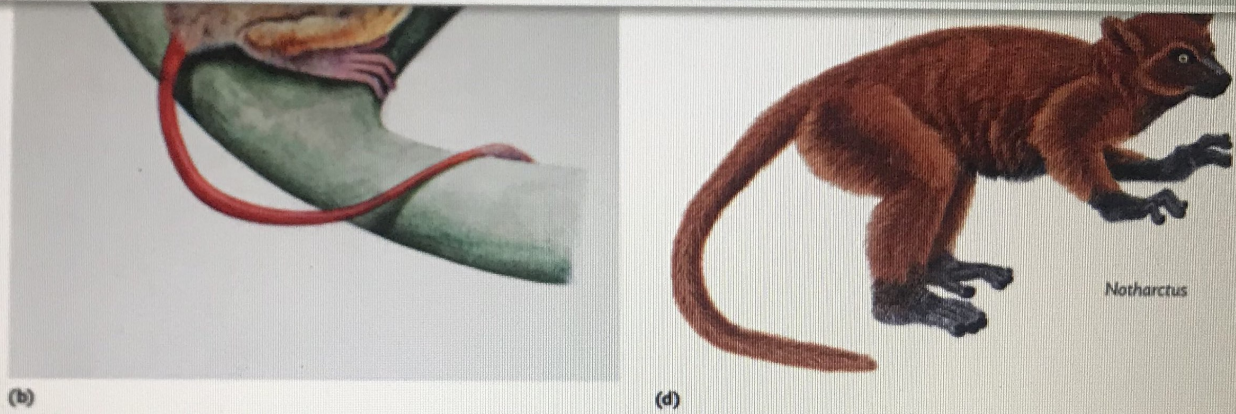
### **Eocene Euprimates: The First True Primates**

Far better contenders for earliest primates are the **Euprimates** (meaning “true primates”), which first appeared at the start of the Eocene, as early as 56 mya. Euprimates consisted of two closely related, highly successful groups: the **adapids** and the **omomyids**. Their fossils are found in the western United States, western Europe, Africa, and Asia and are the most common early primate fossils—accounting for about 40% of all species from the Early Eocene, or about 200 species (**Figure 9.6**). Given the vast number of their fossils that have been collected—on the order of 100,000—anthropologists have an excellent picture of their physical description and their adaptive circumstances.

Were they primates? Almost certainly. Unlike the plesiadapiforms, adapids and omomyids had clear primate characteristics: the postorbital bar and convergent eye orbits, long digits with opposability for grasping, digits with nails (not claws), nonspecialized teeth, and a large brain relative to body size. These features indicate that vision was essential to their adaptation, they were agile and tree-dwelling, their diet was not as specialized as that of the

plesiadapiforms, and they were smarter than the earlier animals. Their body sizes were small but highly varied. Adapids were about the same size as some modern lemurs. One of the largest, *Notharctus*, weighed about 7 kg (15 lb). *Adapis*, known from many skulls and other parts of the skeleton, weighed a little more than 1 kg (2 lb). The adapids' incisors were flat and vertical, similar to those of many living anthropoids (Figure 9.7). In addition, like anthropoids, adapids had pronounced sexual dimorphism in body size and in canine size, some had lower jaws with two fused halves, and some had relatively short foot bones.





**FIGURE 9.6**

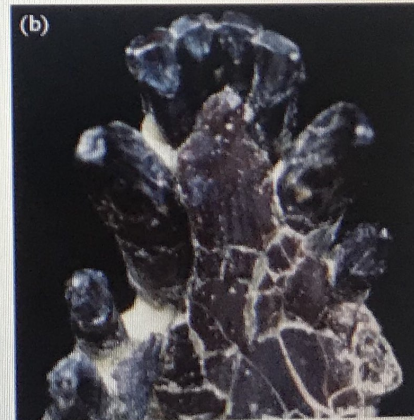
**Omomyids and Adapids** These two main groups of Euprimates are related to tarsiers and lemurs, respectively. Unlike plesiadapiforms, omomyids and adapids are considered true primate ancestors because they possess many primate traits. (a, b) Omomyids, such as *Shoshonius* (shown here), had large eyes and large eye orbits on the front of the skull, grasping hands and grasping feet, and a reduced snout. Like tarsiers, these earliest primates were nocturnal. (c, d) Adapids, including Cuvier's *Adapis*, also had forward-facing eyes. However, adapids like *Adapis* and *Notharctus* were diurnal and had longer snouts than omomyids.

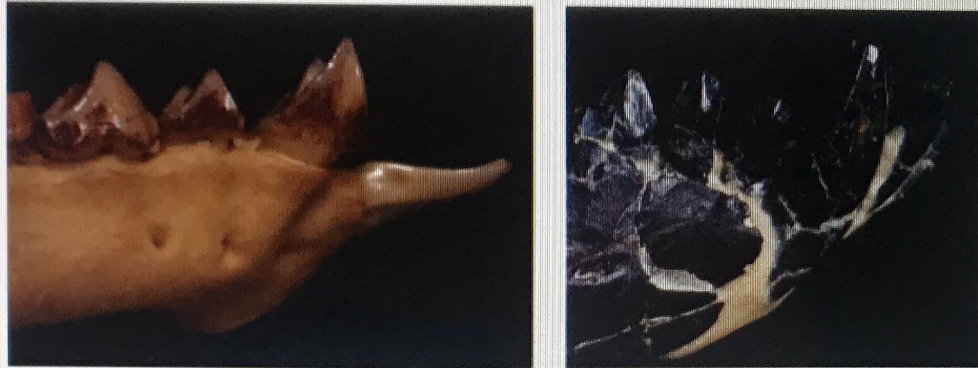
The omomyids differed from the adapids in having large and projecting central lower incisors, small canines, and wide variation in the other teeth. Unlike most adapids (and sometimes like living tarsiers), omomyids had a short skull, a short and narrow snout, and large eye orbits. Their large eye orbits held huge eyes adapted for night vision. Like the adapids, the omomyids consisted of widely diverse species and have left behind a great number of fossils, facts that speak to their high degree of success throughout the Eocene epoch.

epoch.

From what primitive mammalian group did the adapids and omomyids evolve? Most of the plesiadapiforms are unlikely ancestors for the Euprimates because they either went extinct before the Eocene or were too specialized to have given rise to Eocene primates.

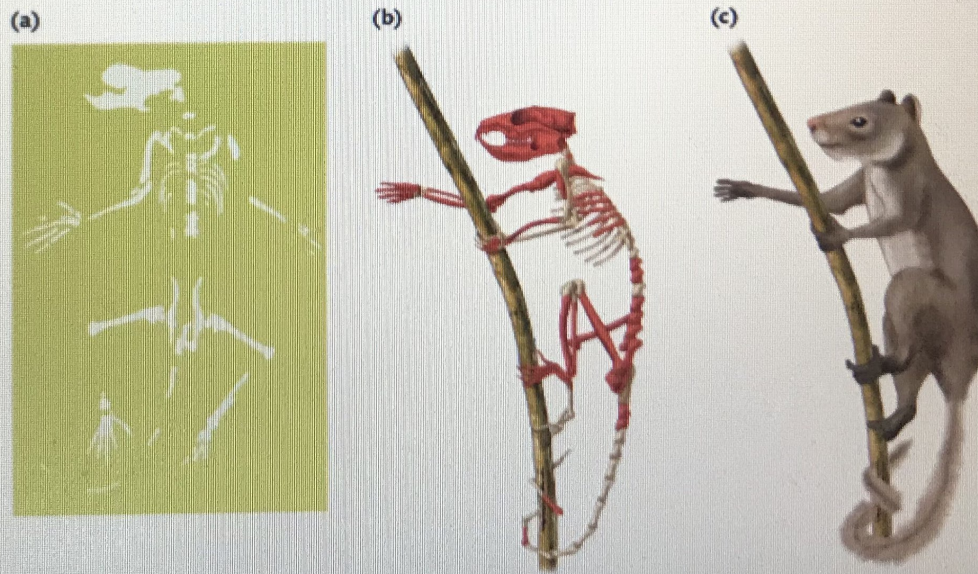
However, one plesiadapiform, *Carpolestes*, whose skeleton was found in Wyoming's Bighorn Basin, had a number of characteristics that would be expected in a transitional animal leading to what were clear primates later in time. *Carpolestes* had a grasping foot, made possible by an opposable big toe; it had long, grasping fingers; and it had a nail on the end of the first foot digit (**Figure 9.8**). This animal may be the link between Proprimates of the Paleocene and Euprimates of the Eocene.





**FIGURE 9.7**

**Incisor Variation** (a) In modern lemur species, the lower incisors form a dental comb that projects horizontally from the mandible. (b) This feature was absent, however, in adapids, whose more vertical incisors resembled those of living monkeys and living apes.



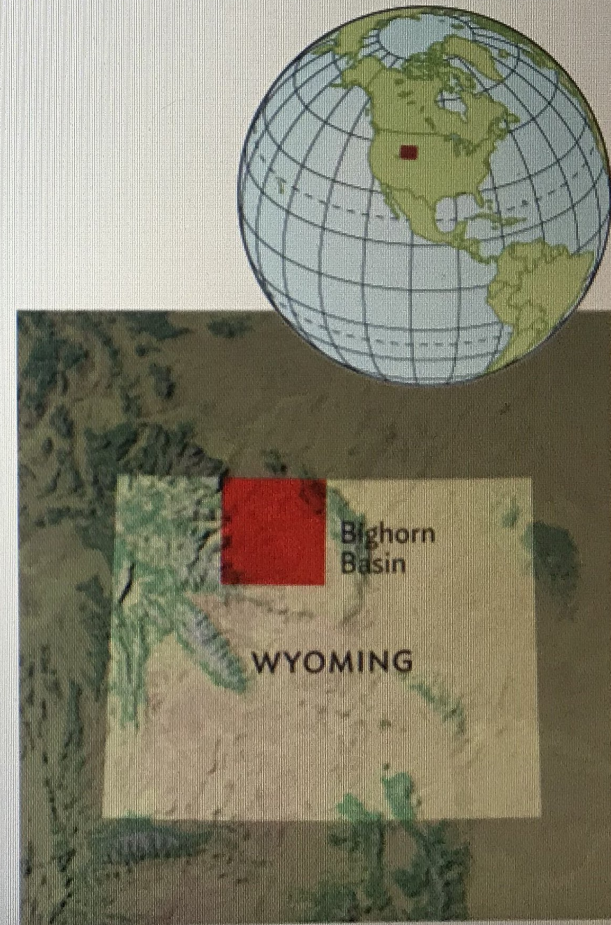
**FIGURE 9.8**

**FIGURE 9.8**

**Carpolestes simpsoni** (a) Fossilized remains such as these suggest that this species of plesiadapiforms is a link between primatelike mammalian ancestors and the earliest true primate ancestors. (b) In this reconstruction of the full skeleton, the fossilized remains are highlighted. (c) This reconstruction depicts what *Carpolestes* might have looked like in life.

The extinction of the plesiadapiforms at the end of the Paleocene and the appearance of Euprimates at the beginning of the Eocene coincided with a profound period of global warming. A rapid temperature increase around 55 mya created tropical conditions virtually everywhere around the world. The resulting creation of new habitats triggered an adaptive radiation of modern-appearing primates, the Euprimates. In particular, the high global temperatures and high global humidity led to an expansion of evergreen tropical forest, the environment that made possible the growth of many mammalian groups, including the primates.

**The Anthropoid Ancestor: Euprimate Contenders**



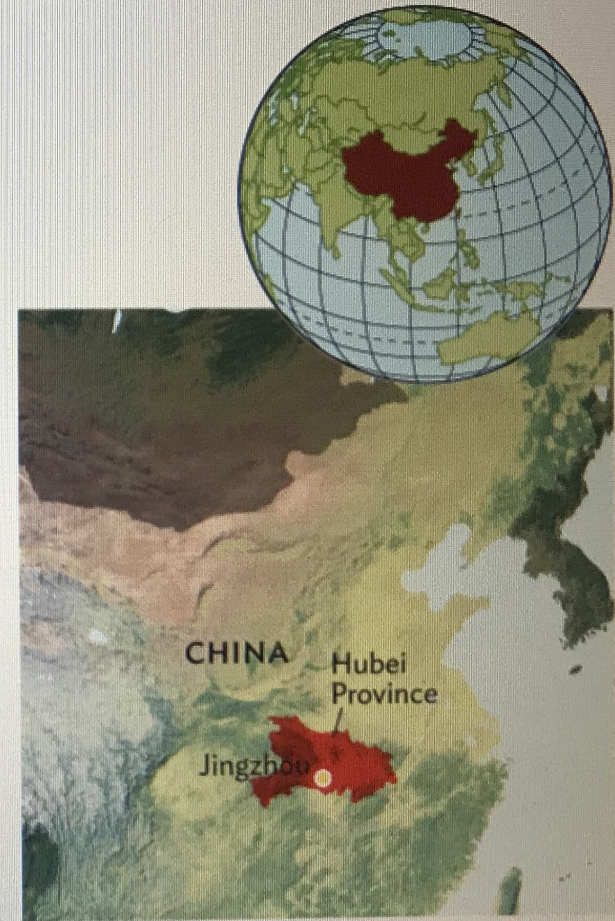
## The Anthropoid Ancestor: Euprimate Contenders

Like the Paleocene Proprimates preceding them, many of the Euprimates went extinct, likely owing to a major change in climate involving a cooling trend, causing a change in habitat at the end of the Eocene. Some of them may have provided the ancestral base for strepsirrhines and haplorrhines. Based on the kind of skull and tooth evidence described earlier, Philip Gingerich has made the case that adapids represent the ancestral group for living lemurs and anthropoids, with lemurs evolving a tooth comb (missing in adapids) and anthropoids not evolving the tooth comb. Their flat incisors, general similarity with anthropoids, and great diversity suggest that adapids had an evolutionary relationship with anthropoids. However, some (or even all) of adapids' anthropoid-like features could simply be unevolved (primitive) traits of all primates. If that is the case, then an ancestral-descendant link between adapids and later primates would be difficult to prove.

The American anthropologist Frederick Szalay sees a strong resemblance between omomyid fossils and living tarsiers, and a greater similarity between tarsiers and anthropoids than between lemurs and anthropoids. Therefore, he regards the omomyids as more likely candidates for the ancestry of anthropoids than are lemurs. However, the anatomical similarities between omomyids and tarsiers are more suggestive than definitive. No single characteristic links these Eocene primates with anthropoids. While the adapids or omomyids may be ancestral to anthropoids, the lack of clear

links these Eocene primates with anthropoids. While the adapids or omomyids may be ancestral to anthropoids, the lack of clear transitional fossils between these archaic primates and later primates makes it unclear what the anthropoid ancestor was more than 40 million years ago.

Clues to the characteristics of the early haplorrhines are seen in a remarkably well-preserved skeleton of an early primate, dating to 55 mya and known as *Archicebus* (Figure 9.9). Discovered in an ancient lake bed in the Jingzhou area of the Hubei Province, China, by a team led by the Chinese paleontologist Xijun Ni, this primate combines features of anthropoids and tarsiers. The presence of this primate in China at such an early date indicates that haplorrhines may have originated in Asia. Although *Archicebus* may not have been the first haplorrhine, it emerged very close to the split between strepsirrhines and haplorrhines. The bones of its heel and ankle resemble those of monkeys. Its skull resembles that of tarsiers, with small eye orbits and a short snout. In addition, the cusps on the molars are high and pointed, similar to what is seen in tarsiers. This mosaic of features suggests that haplorrhines originated at 55 mya on the boundary



seen in tarsiers. This mosaic of features suggests that haplorrhines originated at 55 mya, on the boundary between the Paleocene and the Eocene. It also suggests that the first haplorrhines were diurnal (and therefore had these small eye orbits), arboreal (and therefore had these foot, hand, and limb structures), and primarily insectivorous (as tarsiers are today). And, in contrast to their great evolutionary significance, the earliest-known primates appear to have been tiny. *Archicebus* is estimated to have been even smaller than the mouse lemur (the smallest primate today), weighing only about 28 g (1 oz) and easily fitting into the palm of your hand.

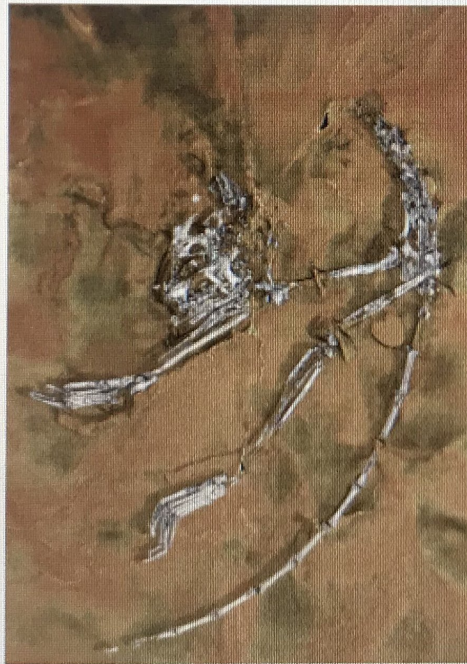


FIGURE 9.9

*Archicebus*. This skeleton and reconstruction of *Archicebus* show its

**FIGURE 9.9**

**Archicebus** This skeleton and reconstruction of *Archicebus* show its combination of anthropoid and tarsier features. Its heels and ankles resemble those of monkeys, whereas its small eyes and short snout resemble those of tarsiers.

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**HOW DO WE KNOW**

# THE FAYUM DEPRESSION

## HEARTLAND OF ANTHROPOID ANCESTORS

The Fayum Depression, the region located on the eastern edge of the Sahara Desert in North Africa, first came to paleontologists' attention in the late nineteenth and early twentieth centuries. Among the various fossils discovered at that time was a primate, the parapihceid *Apidium*, first recognized and reported on in 1908 by the eminent American paleontologist Henry Fairfield Osborne of New York's American Museum of Natural History. To Osborne and his contemporaries, it was clear that the Fayum was special—it held the record of the first anthropoids.

Unfortunately, owing to various events and circumstances, including the Fayum's remoteness and desolateness, no substantive work occurred there

Fayum's remoteness and desolateness, no substantive work occurred there during the next five decades. While on a visit to the American Museum of Natural History in the 1950s, a young graduate student, Elwyn Simons, got a firsthand impression of the fossils collected 50 years before. He concluded that the Fayum deserved another look to address one of the most important questions in biological anthropology: *What were the first higher primates?* *Apidium* had all the makings of a higher primate, and where there was one fossil, Simons decided, there had to be more.

In 1961, Simons went to the Fayum for the first time to collect enough fossils to answer this question and to lay the groundwork for future work at what he hoped would prove an important site. During that trip and many more over the next four decades, Simons found more than 1,000 fossils of ancient primates, dating from the Late Eocene and Early Oligocene, in the area of the Fayum called the Qatrani Escarpment. By studying these fossils, he and his collaborators learned that the first higher primates had all the traits one would expect. In particular, the teeth morphology indicated that these primates ate fruit and seeds. That is, the low, round cusps on the molars reflected the primates' ability to crush and pulp the fruit and seeds. (By contrast, the molars of primates that eat leaves tend to have tiny crests for shearing the leaves.) Simons and his

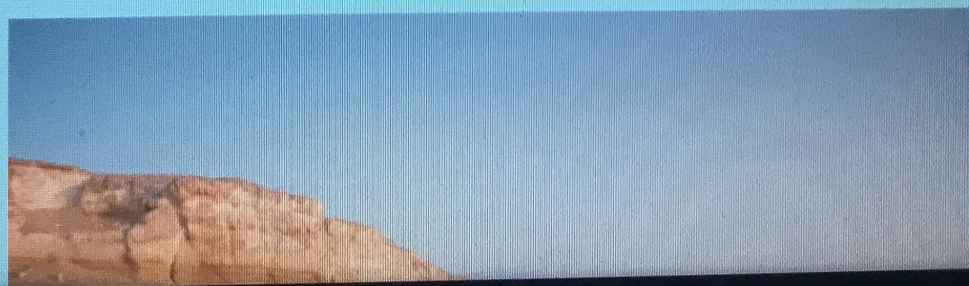


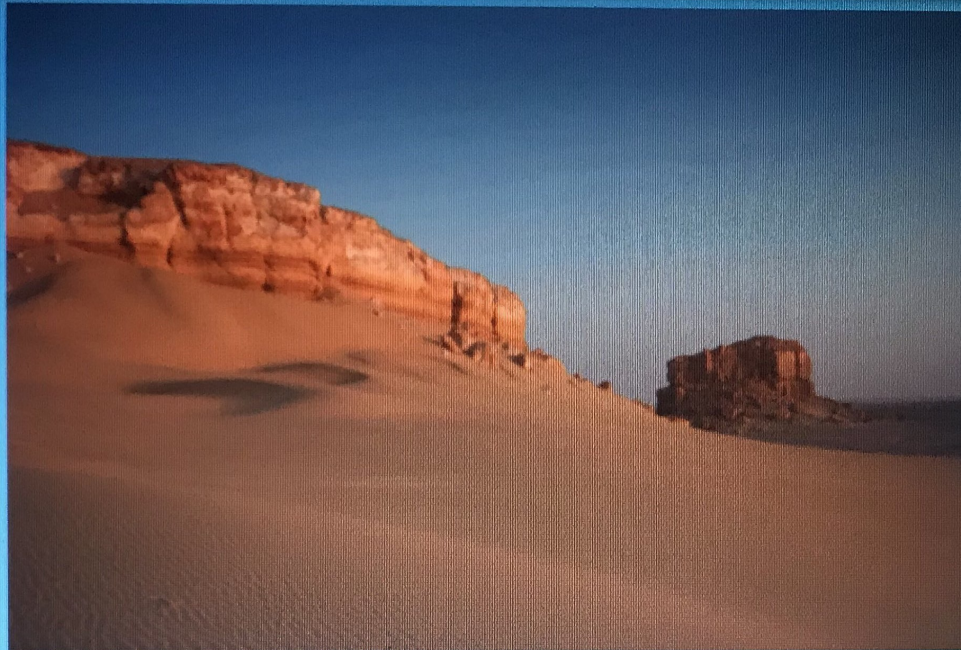
for shearing the leaves.) Simons and his collaborators hit the paleontological jackpot with their discoveries: the Oligocene Fayum primates proved to be the first irrefutable higher primates, with lots of anatomical details to reveal their adaptations.



Situated in the Sahara Desert by the Nile River, Egypt's Fayum region has been a great source of paleoanthropological research, yielding numerous fossils, including those of primates.

Simons also wanted to better understand the ecological context for the higher primates' evolution. *What did the setting look like? What other kinds of animals were living at the same time and the same place?* These questions were tough to answer: they involved the collaboration of many other experts with varying interests, and they required the collection of many thousands of fossils representing both animals and plants. Through careful excavations, exact recording of fossils' locations, and precise dating of fossils' contexts through radioisotope methods (discussed in chapter 8), Simons and his colleagues constructed a highly detailed picture of the Oligocene landscapes in which the first apes lived. Painstaking research enabled these scientists to answer long-standing questions and to produce one of the most comprehensive pictures of past habitats for any time in any place in the world.





This section of the Fayum became a primary focus of research through Simons, who wished to find evidence of more fossil primates, such as *Apidium*. The exposure of geologic strata enabled researchers to access deposits from millions of years ago.





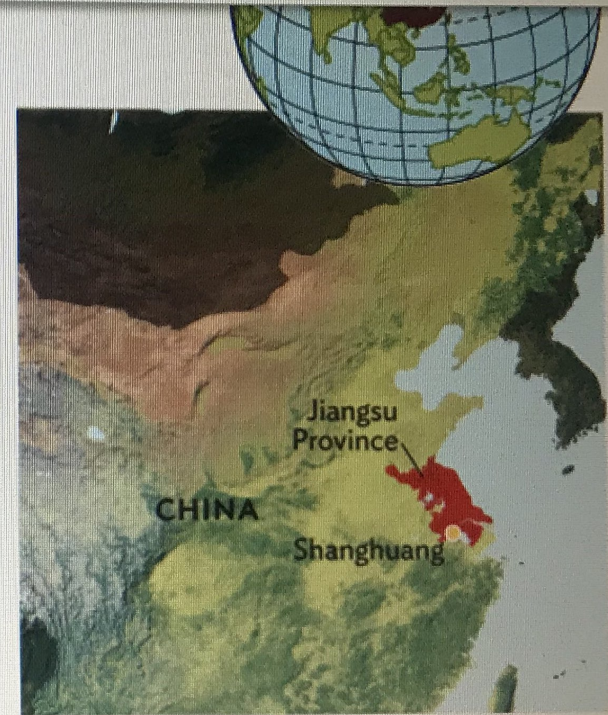
One way in which paleoanthropologists search for fossils in the Fayum is to sweep away layers of sand. Here, the American paleontologist Daniel Gebo exposes fossils of early primates.

### The First Anthropoids

During the Eocene, a group of primates called **basal anthropoids**, whose fossils have been found in Asia and Africa, had the kinds of characteristics that would be expected in an anthropoid ancestor or even the earliest



anthropoid ancestor or even the earliest anthropoid. One of the most interesting basal anthropoids is the remarkably tiny *Eosimias* (meaning “dawn monkey”), found in Jiangsu Province, China, and dating to about 42 mya. It is one of a number of eosimiids found in southern and eastern Asia. Based on their observations of the teeth and the skeleton, especially of the foot bones, the American anthropologists Daniel Gebo and Christopher Beard regard *Eosimias* as the first true anthropoid. Especially convincing about their argument is the strong similarity between the shape and overall appearance of the tarsal (ankle) bones of *Eosimias* and the tarsal bones of fossil and living anthropoids. That is, *Eosimias*'s short calcaneus, or heel bone, was like that of an anthropoid (Figure 9.10). The heel bones are especially similar to the heel bones of South American monkeys, revealing that this primate moved in trees like a monkey. In addition, the upper canine and upper jaw would have given it a monkeylike face.



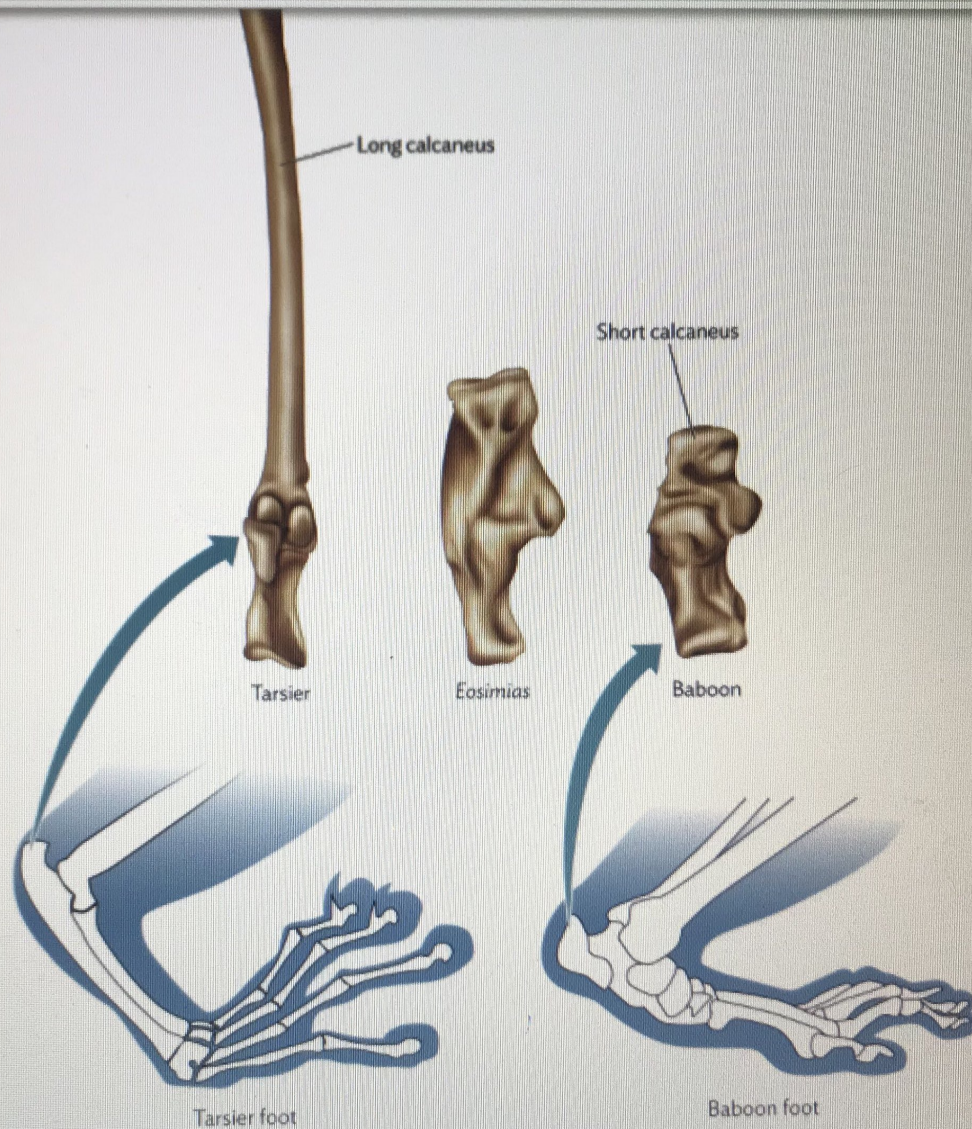


FIGURE 9.10

**Calcaneal Variation** Evidence for patterns of locomotion in *Eosimias* comes from some of the postcranial remains, especially bones of the ankle and foot. *Eosimias*'s calcaneus was more like that of an anthropoid (such as the baboon)

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beginnings of higher primates (**Figure 9.11**). If it is the first higher primate, then either anthropoid ancestry began in Africa or the earlier primates from Asia emigrated to Africa and evolved into the African anthropoids. Based on the limited evidence, it is not possible to say conclusively whether Asia or Africa is the ancestral home of the higher primates, the anthropoids. However, *Eosimias* and *Biretia* have the attributes that would be expected in an anthropoid ancestor. Given the earlier date for *Eosimias*, Asia could be the ancestral home for the higher primates. If so, then Asian basal anthropoids gave rise to the higher primates of Africa.



**FIGURE 9.11**  
**Biretia** Its fossilized remains suggest that this animal was an anthropoid ancestor. For example, its lower premolars, with their two cusps, are structured like those of anthropoids.

This discussion should make clear that the origin of anthropoids is murky. To understand the geographic (Asia versus Africa) and environmental contexts in which anthropoids arose, anthropologists are looking to the increasing fossil record of basal anthropoids and their remarkable diversity. Regardless of their geographic origins, the diversity of basal anthropoids found in both Asia and Africa suggests the beginnings of a tremendous radiation of a highly successful group of mammals.