Miocene Apes

David R. Begun
July in Catalonia can be ideal if you are on the beach, or it can be unbearable if you are in a building with no air conditioning, you have nothing to do, and you are seven. That was my son André’s problem one summer day in 1991. He was patiently waiting for me to finish planning for our 1991 field season at the Miocene hominoid locality of Can Llobateres, about twenty kilometers northeast of Barcelona. When I suggested that we take a trip to the site late that afternoon, André was thrilled. We drove to the site to look over the area. I wanted André to run around a bit, and I gave him a pick to poke around with. I was also looking for the type of sediment we knew from previous work to be most likely to contain fossils. The hard green clays of Can Llobateres are the richest in ape fossils, and I wanted to find a new layer of this sediment. André and I had a great time chopping dirt and I did find some green sediment that looked very promising. The next day the field season began officially. My Spanish colleague and I, along with André and a team of excavators, arrived the next morning, and after setting up I showed my colleague the area I considered most promising. Our picks rose together as we prepared to clear away the layer of overburden covering the fossiliferous sediment. As they struck on both sides of the mark I had made the previous day, a tooth popped out. My colleague’s pick had hit an upper jaw, or maxilla, dislodging the first premolar tooth. As we watched the tooth roll down the slope, we realized we had something significant. Looking at the spot from which the tooth had come, we saw broken bone. When we finished three days later, we had a nearly complete face, by far the most intact specimen of *Dryopithecus* (discussed later) ever recovered from Spain.

Discoveries in paleoanthropology are often a combination of luck and homework. In the case described above, we were lucky to clean a section right where a beautiful specimen was buried. But we also knew that apes had been found at Can Llobateres, and we knew from the nature of the sediments where our chances of finding good fossils were greatest. Sediments reveal details of the environments in which they were deposited. We knew that fossil apes are associated most often with fine grained sediments indicative of very slow moving water, such as that of a river delta, floodplain, or lake margin. In fact, the goals of our project at Can Llobateres were not only to find fossil apes, but also to collect as much information as possible about the environment in which they lived and died, and their geologic age. This information is combined with data on
the anatomy of the fossils to tell us how those organisms lived, what they ate, and how they moved around in their environment.

Our research at Can Llobateres is just one example of many projects on Miocene apes in the last few years. This chapter summarizes research on Miocene apes, its implications for our understanding of ape and human evolution, and the prospects for future work in Miocene ape paleobiology. I will focus on those Miocene apes that are relatively well known and whose general relations to other apes and to humans are reasonably clear.

**BACKGROUND**

Before discussing Miocene apes, a few terms must be defined. Hominoids, or the Hominoidea, is a superfamily in the Order Primates that includes all living apes and humans. The Hominoidea is divided into families, the exact number of which is controversial. Most researchers studying Miocene hominoids recognize two families. One is the Hylobatidae (hylobatids), including the gibbons and siamangs (genus *Hylobates*) of Southeast Asia. The other is the Hominidae (hominids), including the great apes and humans. The great apes include the orang-utan (*Pongo pygmaeus*) from Indonesia, and the African apes—the chimpanzee (*Pan troglodytes*), the bonobo, sometimes called the pygmy chimpanzee (*Pan paniscus*), and the gorilla (*Gorilla gorilla*). Many researchers, and most text books, continue to separate the great apes and humans taxonomically by recognizing a third family, the Pongidae (pongids) for the great apes. This reflects tradition and a bit of anthropocentrism that often prevents anthropologists from seeing the remarkable similarities between humans and great apes. In fact the overwhelming majority of evidence indicates that African apes and humans are more closely related to one another than either are to orangs. To many paleoanthropologists, this means that African apes should not be placed in a separate family from humans. However, since orangs, African apes, and even the earliest members of the human lineage, *Australopithecus*, all look very similar, at least from the neck up, and since all are so different from hylobatids, two hominoid families separating the lesser apes and the great apes and humans is most practical, and most in agreement with current interpretations of hominoid relations (see later discussion).

Living hominoids share a set of characteristics that distinguish
them from other living anthropoids, or higher primates. Their cheek teeth, or molars, have a distinctive arrangement of cusps. Their brains are also somewhat larger than expected for an anthropoid of their size range. But most dramatically, hominoids can be distinguished from other living anthropoids by their postcranial skeleton. All hominoids have skeletons bearing the hallmarks of a suspensory arboreal animal, even those who, like humans, no longer frequent the trees. Hominoids have rather loose but powerful, outwardly facing shoulders, highly specialized elbows to maximize stability in a wide range of positions, mobile wrists capable of adopting a wide range of positions, and long and powerful fingers. All hominoids lack an external tail, and all have specific attributes of the vertebral column, pelvic basin, hip joint, ankle, and foot related to arboreality and more vertical postures.

Apes use these characteristic features to grasp branches and support their body weight from above, unlike most arboreal primates, which move about on top of branches. Humans retain these features because they allow the wide range of arm and hand positions that are crucial to the human way of life, one that is dependent on intensive and elaborate manipulation of the environment.

Hominids (great apes and humans) share many additional characteristics that set them apart from other hominoids (hylobatids). Hominids are all large in body size and relative brain size compared to other hominoids. They have very enlarged front teeth, or incisors, and most have a greatly elongated front part of the palates or upper jaws. They share many other more subtle traits in the dentition and skull, and a large number of features of the postcranium not found in the hylobatids or other primates.

The early history of research on Miocene hominoids has been described in detail elsewhere. Through the 1960s the story of hominoid evolution seemed relatively straightforward. Early Miocene hominoids such as *Proconsul* were thought to be directly related to the great apes (Table 1). Earlier researchers had recognized a closer evolutionary relationship between African apes and humans than between African and Asian great apes. But this view was later abandoned, prematurely as we shall see, and the great apes were lumped together as the descendants of *Proconsul*.

At this time most fossil apes were placed in the genus *Dryopithecus*, a taxon named in 1856 for a lower jaw from France. Many other names had been used for a wide variety of great ape-like Miocene specimens from Europe, Africa, and South Asia, including for example *Sivapithecus* from India and Pakistan, and
Proconsul from Kenya and Uganda. These and many other names were later subsumed under Dryopithecus. One group of fossil apes was excluded from Dryopithecus. These specimens were most often referred to the genus Ramapithecus, and looked more human, mostly by virtue of the thick covering of enamel on their cheek teeth (molars). Figure 1 shows the consensus classification and phylogeny (evolutionary tree) of hominoids as of 1969. It reflects the then accepted division of great apes and humans into “pongids” and “hominids,” with the “dryopithecines” as ancestors of the former, and the “ramapithecines” ancestral to the latter.

Table 1
Fossil Hominoid Taxa and Chronology

<table>
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<tr>
<th>MA</th>
<th>Locality</th>
<th>Taxa</th>
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<tbody>
<tr>
<td>26</td>
<td>Lothidok (Kenya).</td>
<td>Hominoidea (new genus and species)</td>
</tr>
<tr>
<td>21</td>
<td>Meswa Bridge (Kenya).</td>
<td>Proconsul sp.</td>
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<tr>
<td>20</td>
<td>Tinderet series (Kenya-Kuru, Legetet, Chamtwara, Songhor), Napak (Uganda).</td>
<td>Proconsul africanus, Xenopithecus koruensis, Linnopithecus legetet, Limnopithecus evansi, Kaleopithecus songhorensis, Micropithecus clarki, Proconsul major, Dendropithecus macinnesi, Rangwapithecus gordonii, Nyanzapithecus vancouveringorum (N.B. Not all occur at each locality)</td>
</tr>
<tr>
<td>Number</td>
<td>Location</td>
<td>Species</td>
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<td>--------</td>
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</tr>
<tr>
<td>17</td>
<td>Rusinga Island, Mwfangano Island</td>
<td><em>Proconsul nyanzae</em>, <em>Proconsul hesloni</em>, <em>D. macinnesi</em>, <em>L. legetet</em>,</td>
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<tr>
<td></td>
<td>(Kenya).</td>
<td><em>N. vancouveringorum</em></td>
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<td></td>
<td>Kalodirr, Buluk (Kenya).</td>
<td><em>Afropithecus turkanensis</em>, <em>Turkanapithecus kalakolensis</em>, <em>Simiolus</em></td>
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<td></td>
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<td><em>enjiesi</em></td>
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<td></td>
<td>Ad Dabtyah (S. Arabia), Sindhi</td>
<td><em>Heliopithecus leakeyi</em>, <em>Dionysopithecus sp.</em></td>
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<td></td>
<td>(Pakistan).</td>
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<tr>
<td>16</td>
<td>Sihong (China).</td>
<td><em>D. shuangouensis</em>, <em>Platodontopithecus jianghuaiensis</em>, Hominoid indet.</td>
</tr>
<tr>
<td>15</td>
<td>Kipsarimon (Kenya).</td>
<td>2 Hominoida indet.</td>
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<tr>
<td></td>
<td>Maboko, Majiwa, Kaloma, Nachola</td>
<td><em>Nyanzapithecus pickfordi</em>, <em>Mabokopithecus clarki</em>, “Kenyapithecus*</td>
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<tr>
<td></td>
<td>(Kenya).</td>
<td><em>africanus,” Micropithecus leakeyorum</em></td>
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<td></td>
<td>Pasalar (Turkey), Devinsk Nová</td>
<td><em>Griphopithecus darwini</em></td>
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<td></td>
<td>Ves (Slovakia).</td>
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<tr>
<td>13</td>
<td>Çandir (Turkey).</td>
<td><em>Griphopithecus alpani</em></td>
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<td></td>
<td>Fort Ternan (Kenya).</td>
<td><em>Kenyapithecus wickeri</em>, 3 Hominoida indet.</td>
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<td>12</td>
<td>St. Gaudens, La Grive</td>
<td><em>Dryopithecus fontani</em></td>
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<td></td>
<td>(France).</td>
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<td></td>
<td>St. Stefan (Austria), Can Vila,</td>
<td><em>Dryopithecus cf., D. fontani</em>, <em>Sivapithecus indicus</em></td>
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<td></td>
<td>Can Mata, Castel de Barbera,</td>
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<td></td>
<td>Sant Quirze (Spain), Chinji</td>
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<td></td>
<td>(Spain).</td>
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<tr>
<td>11</td>
<td>Ngorora (Kenya).</td>
<td>Hominoidea indet.</td>
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<td>10</td>
<td>Can Ponsic, El Firal</td>
<td><em>Dryopithecus crusafonti</em></td>
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<td></td>
<td>(Spain).</td>
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<tr>
<td></td>
<td>Can Llobateres, Polinya (Spain),</td>
<td><em>Dryopithecus laietanus</em>, <em>Dryopithecus cf,</em></td>
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<tr>
<td></td>
<td>Melchingen, Trochtelfingen,</td>
<td><em>D. brancoi</em></td>
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<td></td>
<td>Ebingen, Wissberg, Eppelsheim</td>
<td><em>Ankarapithecus meteai</em></td>
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<td></td>
<td>(Germany), Yasssioren (Turkey).</td>
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<tr>
<td>9</td>
<td>Rudabánya (Hungary), Mariathal</td>
<td><em>D. brancoi</em></td>
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<tr>
<td></td>
<td>(Austria), Salmendingen</td>
<td></td>
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<tr>
<td></td>
<td>(Germany), Udabno (Georgia).</td>
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Three more recent developments in paleoanthropology have completely undermined this view of hominoid evolutionary history. Interpretations or hypotheses in paleoanthropology, as in other sciences, are subject to testing made possible by new discoveries and new techniques for generating data. A field in which ideas are always changing in the face of new discoveries is exciting and dynamic; method is more important than interpretation. A field in which interpretations never change, hypotheses are never falsified, and theories are unaffected by new data, is not much of a science at all.

Of the three recent developments, two fall into the category of new techniques, while the third is categorized as new discoveries. The first development, relatively new to paleoanthropology but with a long history in biology, is molecular systematics. Since the turn of the century, researchers have been attempting to reconstruct evolutionary history using molecules rather than morphology. In the 1960s a number of researchers had concluded on the basis of work on proteins that humans were more closely related to African apes than to orangs, as Huxley had suggested a century earlier on the basis of anatomical comparisons. The antiquity of the split between apes and humans was also dramatically different according to the molecular evidence. Sarich and Wilson estimated that the split could not have occurred more than three to five million years ago, whereas most paleoanthropologists at the time, recognizing *Proconsul* as a great ape ancestor, placed the split some-
time before the evolution of this form, at least twenty million years ago. Though Sarich’s molecular clock is not widely cited today, his estimate is probably much closer to the truth than the estimate based on Proconsul. Modern research in molecular systematics now shows, based mostly on DNA sequencing, how very closely related we are to the African apes and maybe more specifically to the chimpanzee.10

The second development, again new to paleoanthropology but with a longer history in paleobiology, is cladistics. Cladistics or
phylogenetic systematics is an approach to biological classification that is explicitly evolutionary. All organisms must be classified according to their evolutionary interrelationships. Organisms placed together in a group, or taxon, must be more closely related to the other forms in that taxon than to any organism in another taxon. So, for example, African apes and orangs cannot be grouped to the exclusion of humans, because African apes are more closely related to humans than they are to orangs. This is the main reason the taxon Pongidae is no longer used by many. Taxa like the Pongidae are paraphyletic, meaning they fail to include some lineages, like humans. Including humans with the great apes changes the name of the taxon to Hominidae, because Hominidae was named first. Cladistic methodology provides an explicit protocol for determining ancestor-descendant relationships. The main effect of the application of this method in the analysis of Miocene hominoids has been a thorough re-evaluation of the evolutionary significance of the characteristics used to reconstruct evolutionary relations. Characteristics once thought to indicate a close evolutionary relationship among the great apes, such as large, elongated faces, large canine teeth, very elongated forelimbs, short hindlimbs, and others, are now recognized as primitive characteristics that were also present in the ancestors of humans. Therefore they do not distinguish the human lineage from that of the apes. In contrast, other characteristics, such as well-developed brow ridges, elongated crania, a reduced number of wrist bones, and other details of cranial and postcranial anatomy found only in African apes and humans, suggest that these forms share a period of common ancestry not shared by the orang. Cladistic methods allow researchers to distinguish characteristics indicative of a close evolutionary relationship, or derived characteristics, from those that are more primitive. This type of revision has lead to substantial changes in interpretation of the pattern of relationships among Miocene apes.

The third development of importance to Miocene hominoid research has been new discoveries. The old view of a dichotomy between the “ramapithecines” and the “dryopithecines” has been completely rejected on the basis of new discoveries of both groups. As described later in this chapter, new fossils from Pakistan show that Ramapithecus and Sivapithecus are in fact the same genus. New discoveries of Proconsul, Dryopithecus, Sivapithecus, and completely new forms reveal the pattern of hominoid diversity in the Miocene to be very different from the simple tree that was the consensus in 1969. Figure 2 is a revision of Miocene hominoid classification.
Based on the developments noted earlier. For the rest of this chapter, I will describe these new discoveries and their implications for the evolutionary history of the great apes and humans.

### Figure 2
One Interpretation of Relations among Fossil and Living Hominoids

Instead of arranging taxa in an evolutionary tree, most researchers today prefer dendrograms such as this one, which arrange taxa based on relations but avoid speculations about ancestors and descendants. Note, for example, that *Proconsul* is not ancestral to other forms; it simply branched off first. The common ancestor of *Proconsul* and other hominoids is represented by node A, which is not a named taxon but a hypothetical ancestral form sharing characteristics of both *Proconsul* and other hominoids. In this phylogeny, *Sivapithecus, Lufengpithecus,* and *Pongo* share a common ancestor at C not shared by any other taxon. They are thus most closely related to one another, and related in the same way to all other taxa, with which they are linked at B. Similarly, *Dryopithecus* shares a common ancestor with *Ouranopithecus* at E, and both share an ancestor with the African apes and humans at D. Humans (including *Australopithecus*) share a common ancestor with chimps (Pan) at F, and are therefore more closely related to chimps than either are to gorillas. See text for discussion.
The earliest well-documented Miocene hominoid is *Proconsul*, from sites in Kenya and Uganda up to about twenty Ma (mega-annum, or millions of years ago). One of the most important of these localities is Songhor in southwestern Kenya, near Lake Victoria. Songhor is thought to be about nineteen Ma. Many fossil hominoids are known from Songhor and nearby sites, including species of *Proconsul*, *Rangwapithecus*, and other smaller forms of very unclear evolutionary affinities (see Table 1). Most are probably related to *Proconsul*, but some, like *Dendropithecus*, may represent a different kind of hominoid, or may not be a hominoid at all.

The specimens from Songhor, apart from a small number of more complete jaws, are fragmentary and include only a few post-cranial remains. However, a bit later in time, between about 17.2 and 17.8 Ma, additional similar-looking primates are found at a site on nearby Rusinga Island, in Lake Victoria. Many of these specimens are more complete and provide most of the information we have about the anatomy and evolutionary relations of *Proconsul*.

The Rusinga specimens attributed to *Proconsul* are slightly different from specimens from the older sites, but are currently assigned to the same genus. Based mostly on the evidence from Rusinga, we know that *Proconsul* was a monkey-like arboreal quadruped. Its limbs were roughly equal in length, and its forelimbs lacked most of the characteristics of modern hominoids related to their suspensory locomotor capabilities. *Proconsul* does have a number of features that seem to foreshadow hominoid post-cranial anatomy. *Proconsul* elbows, for example, include a specialized ridge similar to but less well developed than a ridge in modern hominoid elbows, designed to maintain maximum stability through the range of motion at the joint. Subtle aspects of the wrists and fingers also suggest mobility and grasping capabilities similar to that seen in living hominoids, but again less well developed than in modern forms. The hip joints and innominate, or pelvic bones, of *Proconsul* also suggest some enhanced ranges of mobility foreshadowing the hominoid condition, as do some details of the anatomy of the feet. Most important, the anatomy of
the sacrum, the final section of the vertebral column before the tail, indicates that *Proconsul* was like hominoids in lacking an external tail. Thus, *Proconsul* may have been a more deliberate climber, venturing out on smaller branches and branch ends, and often adopting more vertical postures than living monkeys.

The anatomy of *Proconsul* jaws and teeth suggest that it was a generalized frugivore, or fruit eater, but probably taking in some leaves as well. The incisors are not as large as in modern great apes, which use these teeth for processing foods with tough coverings, but were similar to those of the frugivorous gibbons and many Old and New World monkeys. These forms generally have diets of 50 to 75 percent fruits, grains, nuts, bark, roots, and other plant parts excluding leaves. The pattern of microwear on the molars of *Proconsul* also indicates a diet similar to that of modern frugivores. The brain of *Proconsul* is known from one specimen, a skull from Rusinga Island. It is very primitive looking in overall morphology and size, and was no more advanced than the brains of living monkeys. In fact in some ways it resembles the brains of living prosimians.

All in all, with its generalized monkey-like morphology but subtle ape-like features, *Proconsul* is a good representative of the ancestor of living apes, and possibly of living hominids. It may be that *Proconsul* was already somewhat specialized in its own direction and is not directly related to modern forms, but the common ancestor of modern hominoids must have been very similar to *Proconsul*.

Contemporary with the latest specimens of *Proconsul* from Rusinga is another set of taxa from northern Kenya. These are the somewhat enigmatic forms *Afropithecus*, *Turkanapithecus*, and *Simiolus*. These forms are known from the sites of Kalodirr and Buluk, in the Lake Turkana region of northern Kenya, the same region that has proven so rich in fossil humans. A fragmentary jaw and some isolated teeth from Saudi Arabia originally attributed to *Heliopithecus* may also be *Afropithecus*. Although contemporary with *Proconsul*, these three species are very different in their cranial and dental anatomy from other early Miocene forms, which makes their correct placement among the hominoids very difficult.

*Simiolus* is a very small form with unusual cresty teeth and a primitive postcranial skeleton, lacking a number of characteristics that in *Proconsul* foreshadow the hominoid condition. It may not even be a true hominoid but a descendant of a branch that diverged before the hominoids evolved. *Turkanapithecus* is close in
size to the smallest species of *Proconsul*. The best specimen of *Turkanapithecus* is a partial skeleton with most of the face and teeth and a number of associated postcranial bones.\(^{26}\) *Turkanapithecus* has a more projecting mid-face, the region of the nose, than *Proconsul*, and this is reminiscent of more primitive “pre-hominoids” like the thirty-three-million-year-old genus *Aegyptopithecus* from the Fayum deposits of Egypt.\(^{27}\) Other aspects of the anatomy of *Turkanapithecus* are more similar to *Proconsul*, especially the postcrania, which are very similar in both forms.

*Afropithecus* is close in size to the largest species of *Proconsul*, but has a distinctive cranial morphology, with a mixture of features resembling *Aegyptopithecus* and *Proconsul*.\(^{28}\) The upper incisor region or premaxilla of *Afropithecus* is superficially more like that of modern hominoids, being slightly elongated and large, to house the large, thick, upper incisor teeth. Unlike *Proconsul*, *Afropithecus* molars have thick layers of enamel,\(^{29}\) an extremely hard material that coats the teeth of all primates and of most other vertebrates. This is more like the molars of later more advanced hominoids. The postcrania of *Afropithecus* is nearly indistinguishable from that of *Proconsul*.\(^{30}\) *Afropithecus* was probably an arboreal quadruped that moved above branches, like modern monkeys, but was a strong climber and spent more time in vertical postures than do living monkeys. The dietary adaptations of *Afropithecus* were probably also similar to those of *Proconsul*, though the thicker enamel of the former suggests a more varied diet that included hard or tough objects, such as nuts and fruits with durable coverings, or foods that tend to wear teeth rapidly, such as those obtained from terrestrial sources that incorporate some grit. *Turkanopithecus*, with its more cresty molars, may have relied more heavily on foods that require extensive cutting and chopping, such as leaves, which must be finely chopped to liberate the few nutrients they contain.

The mixture of primitive and more advanced, or derived, characteristics of *Turkanopithecus*, and especially *Afropithecus*, makes it difficult to place these taxa in a phylogenetic or evolutionary scheme. It may be that both are more primitive hominoids than *Proconsul*, as suggested by the facial similarities with *Aegyptopithecus*, or it may be that *Afropithecus* is derived, given the more modern appearance of its teeth. More fossil material is needed to resolve the enigmatic relations of these relatively newly described Miocene hominoids.

At the end of the early Miocene, about 16.5 Ma, few fossil
hominoids are known from East Africa. A small number of fossils similar in morphology to smaller possible relatives of *Proconsul* are known from China and Pakistan. But the record of Miocene apes is relatively barren at that time until about fifteen Ma, at which time a rich record of primates is known from Maboko Island and other nearby localities in western Kenya, close to the early Miocene sites of Rusinga and Songhor. Some of the earliest specimens of true Old World monkeys are known from Maboko, as is a prosimian and several hominoids.

Maboko occurs at the beginning of the middle Miocene, which lasts from about 16.5 Ma to about 11.5 Ma. Along with the early Miocene hominoids that persist at Maboko is a new type of hominoid. This form has thick enamel, like *Afropithecus* and *Sivapithecus*, but more modern looking molars, with less strongly developed cingula than in *Proconsul* and *Afropithecus*. It is most like *Kenyapithecus*, first described from the somewhat younger site of Fort Ternan, also in western Kenya. *Kenyapithecus* is more advanced than early Miocene hominoids in molar morphology but retains many primitive features also found in *Proconsul*, both cranially and, especially, postcranially. However, one important set of differences in the postcranial anatomy of *Kenyapithecus* suggests that it may have been more terrestrial than most other hominoids. Certain characteristics of the shoulder joint in *Kenyapithecus* from Maboko are more like those of terrestrial monkeys such as baboons than are the shoulders of *Proconsul* and other hominoids. The possibility of increased terrestriality in *Kenyapithecus* combined with its thickly enamelled molars suggests a greater dependence on terrestrial sources of food, which tend to contain more grit and therefore tend to wear teeth more rapidly. More will be known about the cranial and postcranial anatomy of *Kenyapithecus* when a large new sample from the Nachola area, west of Baragoi, in northern Kenya is analyzed.

Dentally and postcranially similar hominoids are also known from Europe and Turkey at sites contemporaneous with Fort Ternan. The sites of Čandir and Pasalar, both in Turkey, Devinska Nová Ves (formerly Neudorf) in Slovakia, and Klein Hadersdorf in Austria, have produced cranial and postcranial remains very similar to those of Maboko and Fort Ternan. These forms, called *Griphopithecus*, may, together with *Kenyapithecus*, be the earliest members of the lineage that includes the living great apes and humans. However, the precise placement of this group of hominoids represents a major puzzle in hominoid evolutionary studies.
Griphopithecus and Kenyapithecus have molars and premolars that look more like those of modern great apes than do those of early Miocene forms or those of hylobatids. Yet hylobatids and all late Miocene hominoids (discussed later) have postcranial attributes in common with great apes, all of which reflect the importance of suspensory postures in the trees. So there is a conflict between the evidence for the limbs and the evidence of the teeth.

The earliest substantial evidence of modern hominoid cranial and postcranial anatomy comes at the end of the middle Miocene and the beginning of the late Miocene. In the early Miocene form Proconsul, aside from relatively subtle changes in fore and hindlimb anatomy and the less subtle absence of a tail, modern hominoid postcranial anatomy is not present. At Moroto, a site in Uganda from the middle Miocene, about fourteen Ma, a lumbar vertebra is known which looks more modern than any attributed to Proconsul, suggesting the presence of a great ape with a short, stiff lower back and a broader torso, like modern forms. By the end of the middle Miocene and into the late Miocene, modern great ape anatomy becomes even more evident. Two forms appear at nearly the same time, one in South Asia (India and Pakistan) and one in Europe. The South Asian hominoid is Sivapithecus, and its European contemporary is Dryopithecus. Sivapithecus is known from many specimens from sites in the Potwar Plateau region of India and Pakistan.

The sample of Sivapithecus was formerly divided into several different forms (as discussed earlier) but is now universally accepted as two genera, Gigantopithecus for a small number of large to gigantic specimens and Sivapithecus for the vast majority of the material. Sivapithecus and Gigantopithecus are probably closely related to one another, based on considerable similarities in dental morphology. But only Sivapithecus is well known from cranial and postcranial morphology, so I will focus on this form here. The face of Sivapithecus, known from several palatal specimens and a remarkably complete face, GSP 15,000, is extremely similar to the faces of modern orangs. This is true in details of the structure of the palate or upper jaw, the zygomatics or cheek bones, the orbits and the region between the orbits, and in the forehead or frontal bone. In fact, it was the discovery of GSP 15,000, more than any other development (discussed earlier), that convinced most paleoanthropologists that Sivapithecus was not a "dryopithecine" but an early member of the lineage of the orang. Other discoveries of smaller jaws and teeth from the Potwar plateau convinced most researchers that Len
Greenfield had been correct in recognizing that Ramapithecus was simply small individuals of Sivapithecus. Greenfield concluded that specimens called Ramapithecus differed from Sivapithecus only in size and in having smaller canines with a different morphology. Because the canines of Sivapithecus all looked very similar to those of male great apes, and the canines of Ramapithecus all looked very much like those of female great apes, Greenfield concluded that all specimens of Ramapithecus were in fact females of Sivapithecus, the taxon that had been named first. With the publication of GSP 15,000 it became widely accepted that Sivapithecus (now including Ramapithecus) was a close relative of the orang, and had nothing directly to do with the origins of the human lineage.

The interpretation of Dryopithecus has also changed considerably due to new discoveries. Dryopithecus is now known from cranial and postcranial characteristics to be much more modern-looking than Proconsul, with which it was once grouped (see earlier discussion). Three partial crania and large numbers of jaws, teeth, and limb bones from various sites in Europe (Table 1) show that Dryopithecus has characteristics of the palate, jaw joint, mid face, frontal, and braincase only found in African apes and humans, and one other Miocene hominoid, Ouranopithecus, from the late Miocene of Greece. Ouranopithecus is much larger than Dryopithecus and has many of the same features found in Dryopithecus but in exaggerated form. The Greek form also has many unique features of the face and teeth, and even shares a few traits, such as extremely thick enamel and very small canines, with early humans. Some have suggested that the similarities to humans indicate a close relationship, while others have suggested close affinities to gorillas. However, for a number of reasons, it appears more likely that the similarities to australopithecines occur convergently (that is, they were acquired independently), while the similarities to gorillas are superficial and based on the similar sizes of Ouranopithecus and gorillas.

If the characteristics that link Dryopithecus and Ouranopithecus to African apes and humans indicate a close evolutionary relationship, then these European forms may be more closely related to African apes and humans than are Sivapithecus and the orang. This is almost exactly the opposite of the interpretation of these genera twenty-five years ago, based on a smaller number of fossils, that linked a South Asian form to humans and linked Dryopithecus to a side branch of the great apes.

Dryopithecus and Ouranopithecus both have short faces and
poorly developed brow ridges compared to African apes and fossil humans, but both are very similar to African apes and humans in the details of these areas. Given these differences, the view that *Dryopithecus* and *Ouranopithecus* are more closely related to African apes and humans than is *Sivapithecus* is controversial. *Sivapithecus*, after all, has an elongated premaxilla, the front part of the upper jaw, like all great apes, though it is structurally distinct from all but the orang. The issue will probably not really be resolved until African relatives of the African apes and humans are found in the time period between about ten to five Ma. If these relatives more closely resemble *Dryopithecus* and *Ouranopithecus*, which I consider more likely, the Asian forms would have branched off first. If the African relatives share a similar premaxilla with *Sivapithecus* and the orang, that would suggest the European forms diverged first.

*Sivapithecus*, *Ouranopithecus*, and *Dryopithecus* are all quite distinct from one another in the morphology of their jaws and teeth. *Dryopithecus* has more lightly built jaws and teeth with sharper, more pointy cusps, similar to modern chimps, which are frugivorous in their dietary preferences. *Sivapithecus* and *Ouranopithecus* have more massive jaws, and teeth with lower, more rounded cusps and thick layers of enamel, as in the more primitive forms *Kenyapithecus* and *Afropithecus*. In both forms this suggests the inclusion of harder, tougher, or more gritty objects in the diet, requiring higher bite forces to crack or deform, and/or thicker enamel in response to more rapid wear. These characteristics, which are present in early humans (australopithecines) as well, have also been interpreted as indications of a closer relationship to great apes and humans than to *Dryopithecus*. However, since similar anatomical characteristics also occur in the clearly more primitive early and middle Miocene forms, it seems more likely that these are simply traits that have changed relatively frequently during hominoid evolution. Even among australopithecines, other fossil humans, and modern great apes, the spectrum of jaw and teeth morphology is tremendous, and it is not obvious which type of morphology gave rise to which. In the final analysis, hominid jaw and tooth morphology are reliable indicators of diet, but not for reconstructing evolutionary relationships. In terms of the jaws and teeth, hominids are mostly what they eat.

The postcranial anatomy of *Dryopithecus* and *Sivapithecus* is not so well documented as in *Proconsul* (and is almost unknown for *Ouranopithecus*), but the forelimbs and feet are reasonably well known. Both taxa are modern hominoid-like in the morphology of
their fingers and elbows, which indicate well developed suspensory capabilities and wide ranges of joint mobility with maximum stability. Wrist and foot bones also indicate mobility of the type typical of modern hominoids, but most tend to retain certain characteristics of more primitive hominoids like Proconsul, suggesting that suspensory arboreality may not have been quite so well developed as in modern forms. The hamate, a bone of the wrist, is more similar to modern hominoids in Dryopithecus than in Sivapithecus, mostly due to the configuration of the hamate hook, which is more strongly developed in Dryopithecus and modern hominoids and is probably associated with more powerful wrist and finger flexion. The shaft of the humerus is also more like modern hominoids in Dryopithecus, being slightly curved backwards in side view. This is also thought to be indicative of suspensory arboreality. In Sivapithecus the humeral shaft is bent forwards in side view and has very powerful attachment sites for the muscles of the shoulders. This is most similar to large monkeys such as baboons, and may be related to more terrestriality in Sivapithecus. Both Dryopithecus and Sivapithecus were probably basically arboreal. Dryopithecus seems to have been more hominoid-like, being highly arboreal and suspensory, but also probably retained the monkey-like ability to walk atop the branches. Sivapithecus probably ventured to the ground more often, but did not knuckle-walk, as do the African apes when on the ground. Like Dryopithecus, Sivapithecus was also partly monkey-like, but more similar to terrestrial than arboreal monkeys.

Three other large bodied Miocene hominoids are known, but their relations to other Miocene forms and to living hominoids are even less clearly understood. Otavipithecus is only known from a single lower jaw fragment and a few limb bone fragments. It is of middle Miocene age, and shares characteristics with both early and middle Miocene forms. It is interesting that Otavipithecus comes from Namibia in southern Africa, and is the first Miocene hominoid from this far south. The other two Miocene hominoids are from the late Miocene and are represented by very large samples of fossils, but remain poorly understood because of their unique combinations of anatomical features. These are Oreopithecus from the late Miocene of Italy and Lufengpithecus from the late Miocene of China. Both these forms existed between seven and eight Ma, and are the latest surviving Miocene hominoids, along with the last surviving populations of Sivapithecus.

Oreopithecus, from Monte Bamboli in Tuscany, is known from
more postcrania than any other Miocene hominoid except Proconsul. Many jaws and teeth are also known, as are fragments of the cranium. Oreopithecus has been called a hominoid by some and a monkey by others. Cranially, Oreopithecus is very primitive, with a short face, like gibbons and Proconsul, and a very small brain for its body size. Dentally, Oreopithecus is highly specialized, with a unique combination of characteristics resembling both hominoids and Old World monkeys. It has small canines, like some hominids, but long teeth with very tall, transversely aligned, pointy cusps, like monkeys. Also like monkeys, their upper and lower molar teeth greatly resemble one another. The dentition of Oreopithecus is more functionally than structurally similar to that of Old World monkeys. Both morphologies are probably associated with folivory, or leaf eating, but the differences in the number and position of cusps and cutting ridges, or crests, in each indicate separate origins. Similar kinds of folivore-type teeth are also found in other primates such as New World Monkeys and prosimians.

The postcranial anatomy of Oreopithecus is another matter. Much of one skeleton of an Oreopithecus individual is known, and a number of isolated pieces from other individuals are known as well. These all indicate a highly advanced suspensory hominoid with forelimb adaptations to hanging and swinging below branches comparable to that of living apes. It is clear that Oreopithecus was more advanced in modern hominoid-like postcranial anatomy and behavior than any other Miocene hominoid. More detailed analysis of the entire skeleton of Oreopithecus is necessary to reveal whether it is similar in most details to living hominoids, and therefore probably closely related to them, or whether it differs in a large enough number of structural details to suggest an independent evolution of suspensory behaviors in Oreopithecus, as seems to be the case with the dentition and diet.

Lufengpithecus is represented by over one thousand specimens, mostly individual teeth, but also several large cranial specimens and a small number of postcrania, from the site of Lufeng, in Yunnan Province, China. The postcrania include scraps of forelimb material that appear to closely resemble great apes, much like Dryopithecus and Sivapithecus. Not enough is known to determine what differences, if any, from great apes characterized the postcrania of Lufengpithecus. The teeth of Lufengpithecus are very much like many hominids in overall morphology. The postcanine teeth are most like the orang, which, like Lufengpithecus, has wrinkled or crenulated enamel on its molars and premolars.
however, are very similar to those of *Dryopithecus* and *Ouranopithecus* in being quite tall-crowned and narrow. Certain parts of the face, especially around the nose, eyes, and forehead, closely resemble *Sivapithecus* and the orang, while others, particularly the premaxilla and the space between the orbits, are very different from other Asian forms. So *Lufengpithecus*, like *Oreopithecus*, presents an intriguing combination of characteristics from a diversity of hominoids, making the placement of both in the evolutionary framework of the Hominoidea very difficult at present.

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**CONCLUSIONS**

The results of the last twenty years of research in Miocene hominoids has produced some dramatic changes in interpretations of hominoid evolution. Hominoid evolution is much more complicated than was once thought, with at least twenty-five different genera known from between about twenty to six Ma. This increase in recognized hominoid diversity may prompt cries of “splitting,” but in fact is more in line with the known diversity of primates in other superfamilies, like Old World Monkeys (*Cercopithecoidea*) or New World Monkeys (*Ceboidea*). Living hominoids are but a mere shadow of the former diversity of this group.

Several trends are now apparent in hominoid evolution. Dietary changes are relatively subtle, and involve increased specialization of the front teeth (incisors and canines), probably to increase the ability to process a wider diversity of foods. Modern hominids use their front teeth as tools for removing the various protective coverings of the foods they consume. This ability seems to have developed in the late Miocene. A few hominoids, such as *Oreopithecus* and *Ouranopithecus*, became very specialized in their diets, with unusually enhanced folivore morphology in the former and with huge jaws and teeth suggesting enhanced omnivory in the latter. A more dramatic trend is in the evolution of positional behavior. Monkey-like above branch arboreality imposes limits on the size of animals living in the trees and the ease with which they can move within the canopy. Ape-like below branch arboreality and enhanced limb mobility allows access to smaller branches, where much of the food is. Larger animals have a more difficult time balancing above branches, but can remain in the trees if they can effectively position themselves below branches. The trend to
below branch arboreality and increasing body size is apparent from more monkey-like *Proconsul* to more ape-like *Dryopithecus* and *Oreopithecus*. The late Miocene witnesses the appearance of many new and specialized forms of positional behavior. Although no living hominoid moves about in the same way as did any fossil form, all have much in common in their postcranial anatomy. This suggests that the changes in the postcranial skeleton of late Miocene hominoids was extremely successful and flexible, and has led to the development of such diverse patterns of positional behavior as brachiation, knuckle-walking, and bipedalism characteristic of modern hominoids.

The other major conclusion from recent research in Miocene hominoids concerns our understanding of the relations among living hominoids and the place humans occupy among them. There is now widespread agreement among morphologists and molecular systematists that humans are more closely related to African apes than either are to orangs. Furthermore, it is also becoming apparent that humans and African apes are very closely related to one another, such that the precise order in which each diverged from their common ancestor is very unclear. Molecular systematists have been saying with increased frequency that humans and chimps are most closely related among hominids, though many continue to hold that it is just too close to call. Most paleoanthropologists who focus on morphology believe that chimps and gorillas are closest, citing such specialized similarities as knuckle-walking and thinly enamelled teeth. But as we have seen in this review, the significance of these characteristics is not so clear-cut. Enamel thickness is a poor indicator of evolutionary relationships because it changes so often in response to dietary requirements. Knuckle-walking, which is unique to African apes among living forms, is commonly considered to be a recent specialization of the African apes. A more controversial, but in my mind more likely, view is that knuckle-walking characterized our ancestors too. After all, humans do share unusual features of the hand and wrist only with African apes, such as fewer wrist bones, more stability of the joints of the wrist, and shorter hand and finger bones. One real possibility is that humans retain these characteristics because we evolved from a knuckle-walker that needed them to ensure wrist and hand stability while walking on the knuckles. When humans shifted to two feet we lost many features still found in knuckle-walkers,
while others were suitable to the tasks important to early bipeds, such as enhanced manipulation.

If humans evolved from knuckle-walkers, a strong possibility given that all three of the closest relatives of humans (chimps, gorillas, and bonobos) are still knuckle-walkers, this tells us something about the history of human descent from the trees. Humans apparently went through a two step process, first becoming sometime terrestrial knuckle-walkers, like living African apes, and then committing themselves more completely to the ground. As knuckle-walkers, the common ancestors of chimps and humans probably exploited resources similar to those exploited by living chimps today. Living chimps and humans still exploit the greatest range of resources of any primate; they are able to range over long distances and in diverse habitats, and they can to use tools to help process foods which would otherwise be unavailable to them. Humans probably diverged from chimps when they became committed to the more completely open ecology of the grassland, requiring a more efficient mode of long distance terrestrial locomotion (bipedalism) and perhaps also an enhanced ability to manipulate the environment with their hands, which bipedalism made possible. These positional changes, which are apparent in the very first humans, *Ardipithecus ramidus*, precede most other changes that today separate humans from other animals. The brain, for example, changed very little, at least in external morphology and relative size, until comparatively late in human evolution, after the appearance of the genus *Homo*. Obligate terrestriality was really the major impetus in human origins, and it appears to have a long history going back to our common ancestors with the African apes. Research on Miocene hominoids has produced many new insights into human evolution in the past twenty years, and we can expect many more in the years to come. Much new fossil material is already known and is being studied. These new data will provide grist for the mill in the continuing endeavor to unravel the mystery of human origins.

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**NOTES**


Anatomy of *Proconsul* Phalanges from the Kaswanga Primate Site, Rusinga Island, Kenya.”


39. Ward, Walker, and Teaford, “Proconsul Did Not Have a Tail.”


41. Ward, “Torso Morphology and Locomotion in *Proconsul Nyanzae*.”


49. Begun, “Phyletic Diversity and Locomotion in Primitive European Hominids.”

50. David R. Pilbeam, Michael D. Rose, John C. Barry, and S. M. I.


60. Hennig, Phylogenetic Systematics.


SUGGESTED READINGS


Begun, David R. “Relations among the Great Apes and Humans: New Interpretations Based on the Fossil Great Ape Dryopithecus.” Yearbook of Physical Anthropology 37. A recent interpretation of the relations among Miocene and recent hominoids.

