WHAT ARE THE PRIMATES?

The Primates are an order of mammals consisting of the prosimians (lemurs and lorises), tarsiers, New World monkeys, Old World monkeys, and apes (Table 11.1). They are not very closely related to any other mammalian order, their nearest relatives evidently being the flying lemurs *(Galeopithecus)* and tree shrews (Scandentia). The earliest primate fossils are of late Cretaceous age.

The Old World monkeys gave rise to the apes 33–24 million years ago (mya). The fossil monkey *Aegyptopithecus* (late Oligocene) already had some anthropoid (apelike) characteristics. *Proconsul* (23–15 mya) of eastern Africa was clearly an ape, ancestral to man and the African apes, but unfortunately there are no African anthropoid fossils from 6 to 13.5 mya (Fig. 11.1).

The living apes consist of two groups, the African apes (the gorilla, chimpanzees, and man) and the Asian apes (gibbons and the orang). There is a definite gap between these two groups; the branching apparently took place some 12–15 mya.

TABLE 11.1 Classification of Primates

Order Primates
- Suborder Prosimii
  - Infraorder Lemuriformes (lemurs)
  - Infraorder Lorisiformes (galagos, lorises)
- Suborder Tarsiiformes (tarsiers)
- Suborder Anthropoidea
  - Infraorder Platyrrhini (New World monkeys)
  - Infraorder Catarrhini (Old World monkeys)
    - Superfamily Hominoidea (apes)
      - Family Hylobatidae (gibbons)
      - Family Hominidae
        - Subfamily Ponginae (Pongo orang)
        - Subfamily Homininae (African apes, humans)

These groups of primates were originally recognized on the basis of morphological differences. The validity of these groups and their relationship to each other have been confirmed in recent years by molecular characteristics.

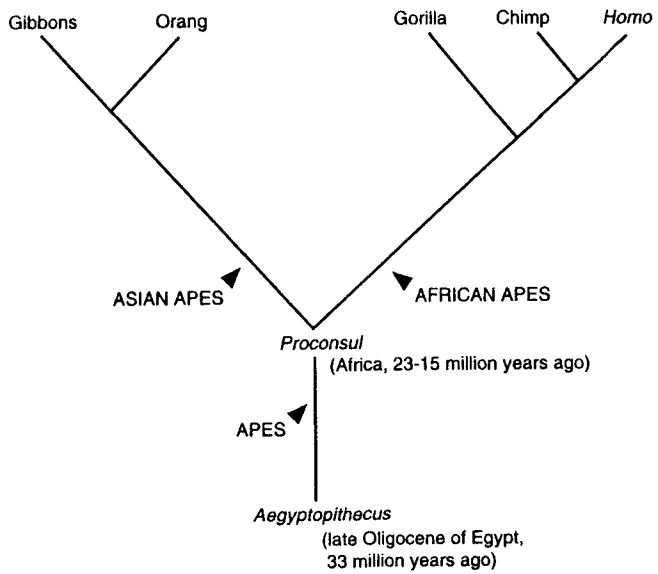

FIGURE 11.1
Phylogeny of the apes.

WHAT EVIDENCE SUPPORTS THE PRIMATE ORIGIN OF MAN?

No well-informed person any longer questions the descent of man from primates and more specifically from apes. The evidence for this conclusion is simply too overwhelming; it consists primarily of three kinds of facts.

Anatomical Evidence. Right down to minor details, humans agree in all anatomical structures with the African apes, particularly the chimpanzee. R. Owen once thought he had found a real difference in the structure of the brain, but T. H. Huxley refuted this claim; the difference is only quantitative, not qualitative. The same turned out to be true for later similar endeavors. The few strictly human characteristics are differences in the proportion of arms and legs, the mobility of the thumb, body hair, skin pigmentation, and size of the central nervous system, particularly the forebrain.

Fossil Evidence. In 1859, when Darwin published his daring findings, no fossils were known that would have supported the gradual transition from a chimpanzeelike ancestor to modern man. Although even today no fossils have yet been found from the period between 5 and 8 mya, during which the branching event took place, numerous fossils dating from 5 mya to the present document the nature of the intermediate stages (see below) between chimpanzees and humans.

Molecular Evolution. One of the great achievements of molecular biology has been to show that macromolecules evolve exactly like visible structural characteristics. Hence a comparison of the human macromolecules with those of apes might shed light on human evolution, and so it does. Indeed, it shows that human molecules are more similar to those of chimpanzees than to any other organism, and furthermore that the African apes are more similar to man than they are to any other kind of primates. The similarity is so great that certain enzymes and other proteins of man and chimpanzee are still virtually identical, for instance, hemoglobin. Others differ slightly, but the difference is less than that between chimpanzees and monkeys.

One can summarize this voluminous anatomical, fossil, and molecular evidence by stating that the very close relationship between man and chimpanzee and other apes has now been convincingly documented. It would be quite irrational to question this overwhelming evidence.

WHEN DID THE HOMINID LINEAGE BRANCH OFF FROM THAT LEADING TO THE CHIMPANZEE?

In other words, how old is the hominid lineage? In the days when man was still considered entirely different from any animal, the branching point was placed way back in time, perhaps at the beginning of the Tertiary, some 50 mya. When more fossils and more and more similarities between man and the African apes were discovered, more recent dates were successively accepted. For quite some time, a date of 16 million years was widely accepted. When a study of the proteins and DNA differences finally permitted the establishment of a molecular clock, the findings suggested that the branching point was as recent as 5 to 8 mya. Subsequent findings by a number of different methods support this date. By these methods it was also established that the branching point between man and the chimpanzee appears to be more recent than that between chimpanzee and gorilla. That is, the evidence now suggests that the chimpanzees are our nearest relatives, and that they are more closely related to man than to gorillas.

WHAT DOES THE FOSSIL RECORD TELL US?

Only a few hominid fossils were discovered prior to 1924 and all represented the most recent stages in hominization, or the rise of the genus *Homo*. These finds were made in Europe, Java, and China. This led to the widespread assumption that man had originated somewhere in Asia, and large expeditions ventured into Central Asia to look for early fossils. Alas, they did not succeed. Even though some perceptive authors had already pointed out that an African origin was much more likely, owing to man's relationship to the chimpanzee and gorilla, it was only in 1924 that the first fossil hominid was discovered in Africa *(Australopithecus africanus)*. Since then, numerous additional finds have been made in Africa, indeed it is only in Africa that fossil hominids older than 2 million years have been found. There is now no longer any doubt that Africa was the cradle of mankind.

The Ascent of Fossil Man

It has been customary in the anthropological literature to tell the story of fossil man in the form of a chronology of the discoveries. It usually began with Neanderthals (1849, 1856), went on to *Homo erectus* (1894 [Java], 1927 [China]), and then to the African discoveries (from 1924 on). For an evolutionist, however, it makes more sense to begin with the earliest fossils and gradually move on to the discoveries of the geologically more recent ones. This is the approach that I adopt.

The chimpanzee lineage, well after its separation from the hominid line, split into two allopatric species. One is the widespread chimpanzee *(Pan troglodytes)*, ranging across all of Africa from the west to the east, and the other one is the bonobo *(Pan paniscus)*, who is restricted to the forests on the western bank of the Congo River in Central Africa. This river separates the two species. In some of its behavior, the bonobo seems to be more similar to humans than is the chimpanzee, but this does not mean that the bonobo was our ancestor. The branching event between chimpanzee and bonobo took place only a few million years ago, long after the hominid and chimpanzee lines had split.

How to Reconstruct the Path from Ape to Man?

One of the tasks of paleoanthropology is to reconstruct the sequence of the changes from ape to man. The early students of fossil man who attempted such reconstructions had been trained as anatomists and were highly qualified to describe these changes. However, conceptually they were not equally well prepared for this task. They were typologists, thinking in terms of a change from "Ape" to "Man." What they wanted to find were the steps in the gradual change of the type ape into the type man. They also had an almost teleological belief in a linear trend "toward more perfection," a progressive trend culminating in *Homo sapiens.*

Alas, the reconstruction of the steps of hominization proved to be very difficult. First of all, the first fossils that were found were the most recent ones. So the path of reconstruction was not from ape to man but from man back to ape. More disturbingly, it turned out to be quite impossible to establish the hoped for smooth continuity. This, of course, was largely due to the incompleteness of the fossil record, but not entirely so, and this is what was so disturbing. As we shall see (see below for details), some fossil types were relatively common and widespread, such as *Australopithecus africanus*, *A. afarensis* and *Homo erectus*, but they were seemingly separated by discontinuities from their nearest ancestors and descendants. This is particularly true for the break between *Australopithecus* and *Homo.*

WHAT IS THE ACTUAL FOSSIL EVIDENCE?

Unfortunately, no hominid fossils—nor such of a fossil chimpanzee—are as yet known for the period between 6 and 13 mya. Thus there is no documentation of the branching event between the hominid and the chimpanzee lineages. To make matters worse, most hominid fossils are extremely incomplete. They may consist of part of a mandible, or the upper part of a skull without face and teeth, or only part of the extremities. Subjectivity is inevitable in the reconstruction of the missing parts. From the beginnings of human paleontology there has been a tendency to compare every fossil with *Homo sapiens.* A fossil (or particular parts of it) was then considered "advanced" or primitive ("apelike"). These comparisons showed that hominid evolution tended to be highly "mosaic." A very *Homo*-like dentition may be associated with rather apelike extremities, and other rather incongruous combinations were also found.

A general text on evolution like this one cannot present the cons and pros of all interpretations of the controversial hominid finds (and virtually all of them are somewhat controversial!). This would be totally bewildering for the nonspecialist reader. What I have done, and will surely be widely criticized for, is to select among the numerous interpretations that one that seemed to me the most likely correct one. The reader must realize that the assignment of each fossil in this treatment is provisional. Any new find may drastically change the situation. Proposals such as the tentative placement of *Homo habilis* with the australopithecines or the immigration of *Homo* into eastern Africa from elsewhere in Africa are particularly vulnerable. It is important in this bewildering situation not to take anything for granted. Tattersall and Schwartz (2000) provide a most helpful account of the variation of hominid fossils. Anthropologists coming into hominid classification from anatomy must remember that taxonomic species names like *afarensis*, *erectus*, and *habilis* do not designate types but rather variable populations and groups of populations.

Our incomplete knowledge of the fossil hominids is highlighted by the fact that no less than six new species of fossil hominids were described in the seven years since 1994. No one has yet attempted to

properly place them in a new hominid phylogenetic tree. What portion of the differences among the various fossils is due to geographic variation cannot be determined on the basis of the few scrappy remains.

STAGES IN HOMINIZATION

Yet, as far as the general trend in human evolution is concerned, the fossil record is of considerable assistance. By making use of the interpretations of numerous authors, but relying particularly on Stanley (1996) and Wrangham (2001), I am developing a sequence of historical narratives that reconstruct the various steps in the history of the change from ape to man. The resulting picture is entirely based on inferences and any part of it may be refuted at any time. But developing a cohesive story is far more instructive than merely compiling a list of unconnected facts. The most important certainty that has emerged from recent studies is that *Homo sapiens* is the end product of two major ecological shifts (habitat preference) of our hominid ancestors. As a result, one can distinguish three stages of hominization:

The Rain Forest Stage	Chimpanzee
The Tree Savanna Stage	*Australopithecus*
The Bush Savanna Stage	*Homo*

The Chimpanzee Stage. Rain forest apes move from tree to tree commonly by brachiation. Their main foods are soft fruits and other soft plant material (leaves, stems, etc.). The small brain and great sexual dimorphism are diagnostic for the apes. They spend most of their life in trees and there is no selection pressure for bipedalism.

The Australopithecine Stage. Around 5–8 million years ago, some species of chimpanzeelike ape succeeded in establishing founder populations in the belt of tree savanna surrounding the rain forest. A huge area of Africa at that time was apparently occupied by the tree savanna and these colonists evolved into the australopithecines. They were apparently immensely successful and presumably occurred wherever there were tree savannas in Africa, even though at present their fossils have been found only in eastern Africa from Ethiopia to Tanzania and in South Africa. There is a single find in Chad (central Africa).

In order to become adapted to this new habitat, these apes had to change remarkably little. At this time the trees were more often some distance from each other and the apes had to adopt bipedal locomotion, but they essentially remained arboricolous and usually slept in tree nests, like other apes. A shift to bipedal locomotion may not be as difficult for a primate as is sometimes believed. I have seen South American spider monkeys move considerable distances bipedally in the Phoenix (Arizona) Zoo. The only other adaptation apes had to acquire was longer and harder teeth, since they had to include tougher plant material in their diet as there was probably a shortage of soft tropical fruit in this more arid habitat. Some anthropologists believe that they discovered the edibility of underground storage organs of plants, such as tubers, rhizomes, and corms, which occur in more arid habitats. Lions, cheetahs, wild dogs, and other carnivores that outrun their prey were rare or absent in the tree savanna, and trees were always available for escape from predators. As a result, the australopithecines had no need to change most of their ancestral chimpanzee characters, such as small size, large sexual dimorphism (males being about 50 percent larger than females), a small brain, long arms, and short legs.

There are two well-documented gracile species of australopithecines: *A. afarensis* in eastern Africa from Ethiopia to Tanzania (3.9–3.0 mya) and *A. africanus* in southern Africa (3.0–2.4 mya) (Fig. 11.2). Both have a small brain of about 430–485 cc. Although they are allospecies, *A. africanus* is younger and more similar to *Homo* except in the proportions of its extremities. Considering that chimpanzees were already quite proficient in tool use, one would expect the same from the australopithecines, but so far no flaked stone tools of theirs have been discovered. Whatever tools they may have made from wood, plant fiber, and animal skins have not survived. There is no reason not to assume that the australopithecines lived in tree savannas throughout Africa.

Australopithecus was largely a vegetarian. Its incisors were larger than those of man, as were its molars, which are considerably smaller in chimps.

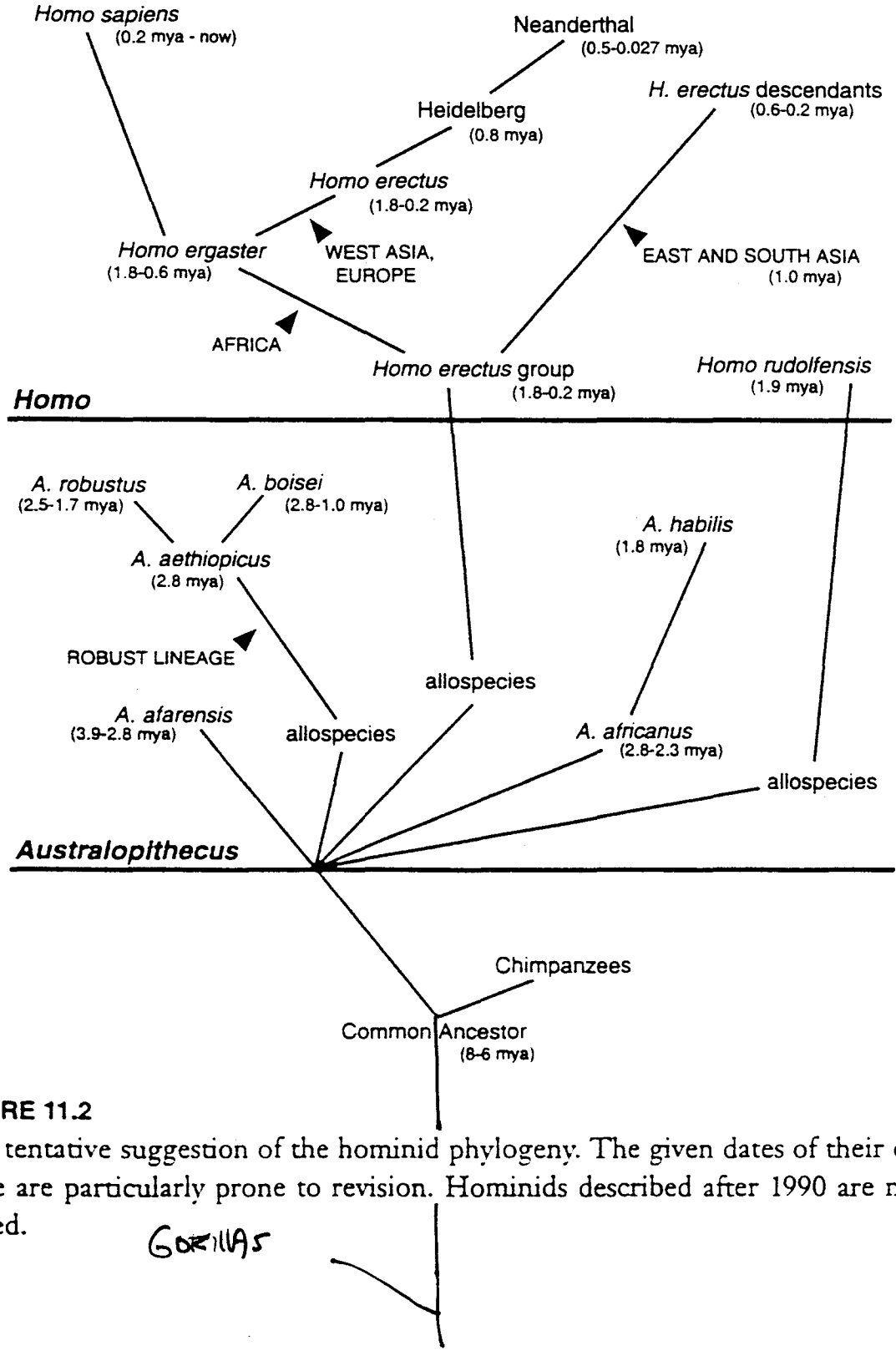

FIGURE 11.2

Very tentative suggestion of the hominid phylogeny. The given dates of their occurrence are particularly prone to revision. Hominids described after 1990 are not included.