

By E. Delson and I. Tattersall

REPRINTED FROM:

Encyclopedia of Human Evolution and Prehistory, 2nd ed; E. Delson, I. Tattersall, J. A. Van Couvering and A. S. Brooks, eds. Garland: New York, 2000

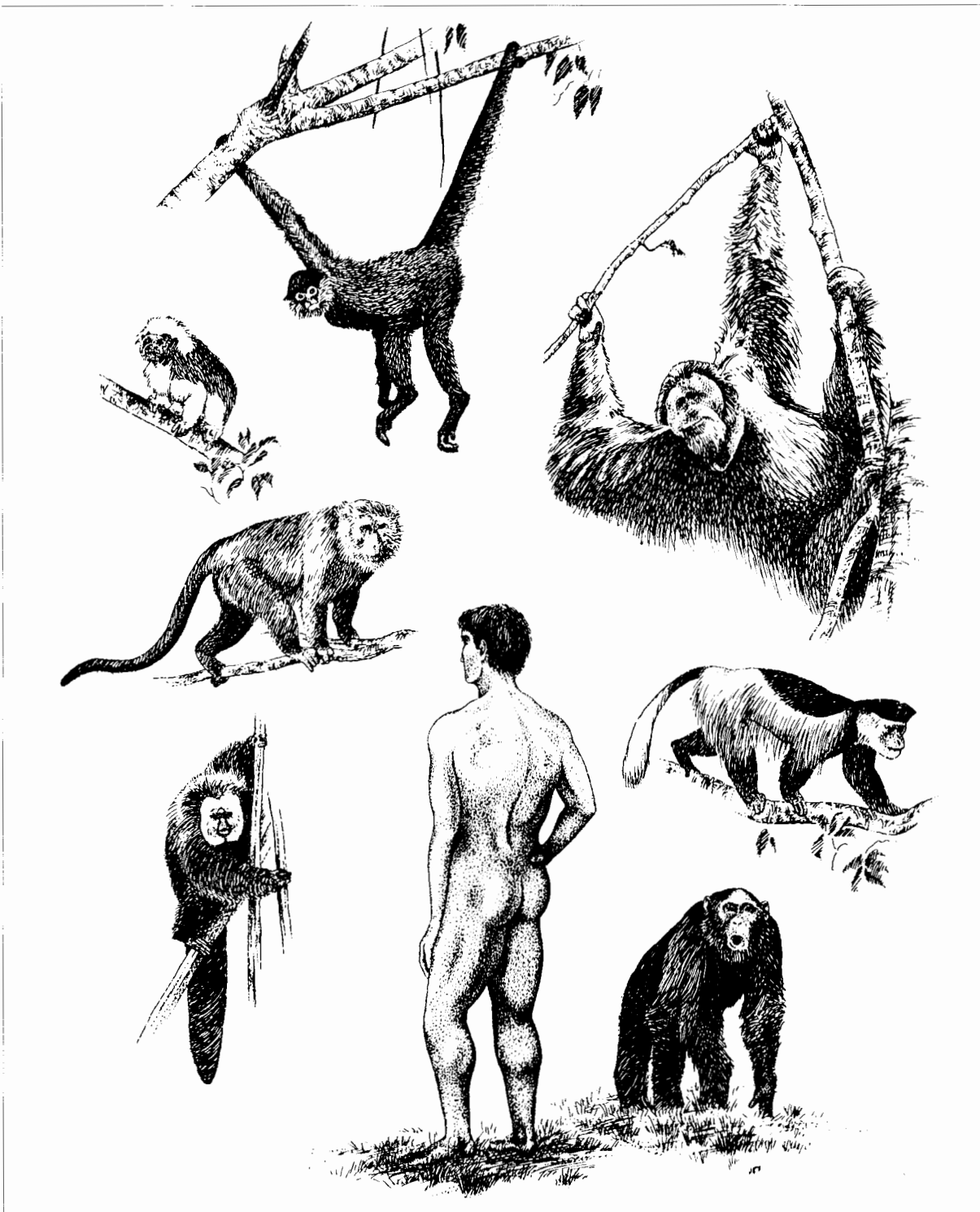
WITH THE COMPLIMENTS OF:

Eric Delson
Department of Vertebrate Paleontology
American Museum of Natural History
New York, NY 10024

Primates

Order of mammals to which human beings and ca. 200 other living species belong. Classification of the group is not entirely settled; for example, all currently accepted classifications divide the living primates into two major groups (suborders), but zoologists differ as to whether *Tarsius*, the tarsier, should be classified with the lower primates (lemurs, lorises, bushbabies) in the suborder Prosimii or with the higher primates (New and Old World monkeys, apes, humans) in the suborder Haplorhini. In the classification adopted for this encyclopedia, the latter arrangement is provisionally preferred. As in the case of any other natural group, what essentially unites the primates is their common phylogenetic origin: All primates are descended from a single ancestor. Since evolution involves change, and Primates (spelled with a capital P and pronounced "pri-MAY-tees" only when used as a proper noun) has diversified considerably from that ancestor, we would not expect that this common origin would necessarily be reflected in the possession of a suite of diagnostic features by all members of the order. This turns out to be the case, at least in features that are observable in the fossil record, and it is probably for this reason that, following W.E. Le Gros Clark, recent students of Primates have generally characterized the order on the basis of several progressive evolutionary trends. Among these are the dominance of the visual over the olfactory sense, with the associated reduction of the olfactory apparatus and elaboration of stereoscopic vision; the improvement of grasping and manipulative capacities; and the tendency to enlarge the higher centers of the brain. Among those primates extant today, the lower primates more closely resemble forms that evolved early in the history of the order, while the higher primates belong to groups more lately evolved.

Trends, however, are of little use in providing a morphological definition of Primates with which the attributes of potential members of the order might be compared. Thus, R.D. Martin has recently reinvestigated this problem, finding that a number of universal or near-universal features do, indeed, demarcate living primates from all other placental mammals. Unfortunately near-universality is more generally the rule than universality, and such features cannot be

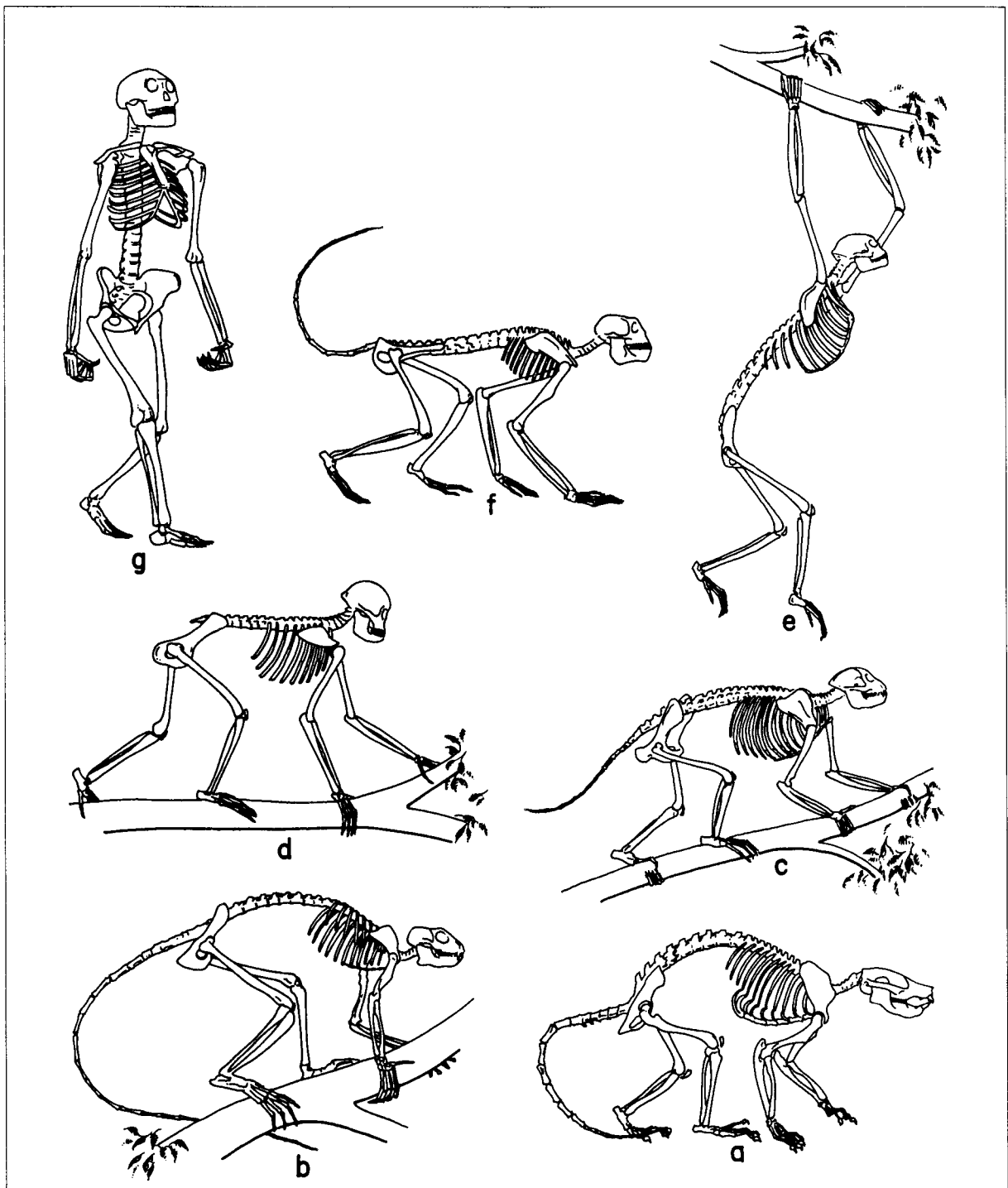


Representative living higher primates. Clockwise from upper left: tamarin (*Saguinus*, *Callitrichinae*); spider monkey (*Ateles*, *Atelinae*); orangutan (*Pongo*, *Ponginae*); colobus (*Colobus*, *Colobinae*); chimpanzee (*Pan*, *Homininae*); human (*Homo*, *Homininae*); saki (*Pithecia*, *Pitheciinae*); macaque (*Macaca*, *Cercopithecinae*). Not to scale; by D. McGranaghan. For lower primates, see illustrations in *STREPSIRHINI* and *TARSIIFORMES*.

used in a rigid morphological definition, even (or especially) when such definition is based, as it must be, on an aggregation of animals already defined as Primates. Moreover, characteristics that do, indeed, definitively demarcate primates from other placentals, such as the possession of a brain that constitutes a significantly larger proportion of body weight at all stages of gestation, are impossible to apply to the fossil record, which is where the questions actually lie; for, follow-

ing the expulsion in the 1970s of the treeshrews from Primates, there has been no doubt about which members of the living fauna belong to Primates and which do not.

There is similarly no question about which typical Eocene (55–34 Ma) and later fossil forms are to be allocated to Primates, since by this epoch “primates of modern aspect” are present in the fossil record, and their aspect is modern enough to allay any doubts as to their phylogenetic affinities.



Skeletons of selected fossil primates. (a) *Plesiadapis tricuspidens* (*Plesiadapidae*); (b) *Smilodectes gracilis* (*Notharctidae*); (c) *Propliopithecus* (= *Aegyptopithecus*) *zeuxis* (*Propliopithecidae*); (d) *Proconsul heseloni* (*Proconsulidae*); (e) *Pliopithecus vindobonensis* (*Pliopithecidae*); (f) *Mesopithecus pentelicus* (*Cercopithecidae*); (g) *Australopithecus afarensis* (*Hominidae*). Not to scale; by D. McGranaghan.

The earliest primates, however, do pose a problem, and opinions have varied about whether the primates of the Paleocene epoch (ca. 65–55 Ma) should, indeed, be admitted to the order. This is because these forms are both adaptively different from, and have no direct evolutionary links with, any living representatives of the order; to express this, they are placed in their own primate semiother, *Plesiadapiformes*. The plesiadapiforms are recognized as primates because of resemblances to later members of the order in their chewing teeth

and locomotor anatomy; these serve quite convincingly to demonstrate the common origin of the two groups, which probably took place toward the end of the Cretaceous period, sometime more than 70–65 Ma. Found in both the Old and the New Worlds, the plesiadapiforms retained clawed hands and feet, possessed large, specialized front teeth, and were probably arboreal in habit. An alternative interpretation is that the plesiadapiforms are more closely related to the living dermopterans, or “flying lemurs,” a group

of Southeast Asian gliding mammals. This implies recognition of a supraordinal taxon Archonta, which would group treeshrews, dermopterans, and perhaps bats with primates (*see* ARCHONTA; CARPOLESTIDAE; EUPRIMATES; FLYING-PRIMATE HYPOTHESIS; PALEOCENE; PAROMOMYIDAE; PAROMOMYOIDEA; PICRODONTIDAE; PLESIADAPIDAE; PLESIADAPIFORMES; PLESIADAPOIDEA; SAXONELLIDAE).

Euprimates

No known plesiadapiform is a satisfactory candidate for the ancestry of the fossil "primates of modern aspect" or euprimates typical of the Eocene epoch. These later primates are grouped broadly into *lemurlike* forms, usually classified in the superfamily Adapoidea (*see* ADAPIDAE; ADAPIFORMES; EOCENE; NOTHARCTIDAE) and *tarsierlike* forms, generally classed as omomyids (*see* ANAPTOMORPHINAE; EOCENE; MICROCHOERINAE; OMOMYIDAE; OMOMYINAE), although this elementary division may ultimately prove to be oversimplified. Eocene primates from both the New World and the Old World already exhibit the trends noted above that mark modern primates as a whole. These arboreal creatures possessed grasping hands and feet in which sharp claws were replaced by flat nails backing sensitive pads; the face was reduced in response to a deemphasis of the sense of smell; the eyes were completely ringed by bone and faced forward, producing wide overlap of the visual fields (hence, stereoscopic vision) and suggesting a primary reliance on the sense of vision; and the brain was enlarged relative to body size when compared with other mammals of the time.

It is possible that the origins of some modern lower primates may be traced back to or through certain Eocene primate genera known in the fossil record. In any event, it is widely accepted that the antecedents of the living primates are to be sought somewhere within the Eocene primate radiation, even where the details of this ancestry remain unclear. In North America, the descendants of the Eocene primates gradually disappeared following the close of the epoch, while virtually all fossil lower primates from later epochs in Africa and Asia are quite closely related to the modern primates of those areas (*see* GALAGIDAE), except for *Afrotarsius* from the Fayum (Egypt) and possibly for a fragmentary strepsirhine recently found there. The bulk of living strepsirhine primates, known as the lemurs, survive in Madagascar. Since the recent (less than 1.5 Ka) arrival of humans in that island, many of the Malagasy primates have become extinct, notably the large-bodied climber-hanger *Palaeopropithecus*, the koalalike but huge *Megaladapis*, and the baboonlike *Archaeolemur* (*see* ARCHAEOLEMURIDAE; LEPILEMURIDAE; PALAEOPROPITHECIDAE). Extant Malagasy primates are grouped into five families (*see* CHEIROGALEIDAE; DAUBENTONIIDAE; INDRIIDAE; LEMURIDAE; LEPILEMURIDAE). Other living strepsirhines include the lorises of Asia and Africa (*see* LORISIDAE) and the bushbabies of Africa (*see* GALAGIDAE). All extant strepsirhines possess dental scrapers or tooth combs (*see* LEMURIFORMES; TEETH), and all retain the primitive mammalian external nose, with a moist, naked rhinarium and associated structures. Additionally, all are united by possessing a toilet (grooming) claw on the second digit of the foot (*see*

LEMURIFORMES; STREPSIRHINI). All strepsirhines possess grasping extremities, although their manual dexterity is generally inferior to that of the higher primates, in comparison with which their brains also tend to be relatively small.

Anthropoidea

The higher, or anthropoid, primates today are the dominant forms in all areas other than Madagascar. Their ultimate ancestry is obscure, but most researchers agree that it probably can be traced back toward the omomyid group of Eocene species. Of the living primates, tarsiers are commonly regarded as closest to anthropoids in details of nasal structure and placentation, the partial rear closure of the orbit, and the bony ear. In turn, some omomyids share dental, cranial, and postcranial structures with tarsiers, and some of the less extreme forms preserve incisor teeth that foreshadow the pattern characteristic of ancestral anthropoids (*see* EOSIMIIDAE; HAPLORHINI; TARSIIDAE; TARSIFORMES).

Opinion varies more widely on the paleogeographic wanderings of early anthropoids, with two main views current: (1) a broadly protoanthropoid stock of omomyids was distributed in western North America and eastern Asia (where a later Paleocene species has recently been recognized), which diverged by the Early Eocene into two southward-expanding lineages: one entered South America to evolve into the platyrrhine New World monkeys, while the other spread across Eurasia into Africa as the ancestral catarrhines; or (2) a Eurasian protoanthropoid stock entered Africa by the Middle Eocene, where it divided into early catarrhines and a platyrrhine ancestor that rafted or island-hopped across the South Atlantic to reach the neotropics. A third alternative has been proposed in which a poorly known group of protoanthropoids (represented by new finds in Africa and/or Asia) was long distinct from both widespread Eocene taxa and gave rise to the modern lineages in an as yet unknown region. Each hypothesis has both morphological and paleogeographical problems to answer before one can be firmly accepted as more likely, but there is broad agreement on the monophyly of Anthropoidea if not on the date or place of divergence of the two infraordinal clades (*see* ANTHROPOIDEA; CATARRHINI; PALEOBIOGEOGRAPHY; PLATE TECTONICS; PLATYRRHINI).

The platyrrhines include two major divisions in most classifications, but not all researchers agree on the contents of these groups. Here, two families are accepted: the generally small-bodied Cebidae, with a lightly built masticatory system; and the mainly medium- to large-size Atelidae, with more robust jaws and teeth. Early members of both families are known by ca. 20 Ma, and most fossils can be closely linked to living genera. This pattern of *bathyphyly*, the long extension of evolutionary lineages, is a characteristic of the platyrrhines in strong opposition to the more bushy pattern of successive radiations seen in the catarrhines (*see* ATELIDAE; ATELINAE; ATELOIDEA; CALLITRICHINAE; CEBIDAE; CEBINAE; MONKEY; PITHECIINAE).

Living catarrhines are readily divided into the Cercopithecoidea (Old World monkeys) and the Hominoidea (lesser apes, great apes, and humans), but that distinction is not so easy to trace back into the past. Cercopithecooid mon-

keys are characterized by a bilophodont dentition and general skeletal adaptation to quadrupedal life on or near the ground, while hominoids share less derived teeth, a trend to larger brain and body size, and a complex of postcranial features emphasizing forelimb flexibility and suspension.

The earliest Old World anthropoid was once thought to be the later Eocene Burmese *Pondaungia*, but competition for this distinction has increased through the 1990s in the form of several equally poorly known taxa from North Africa and China. More definite are the latest Eocene and Early Oligocene (ca. 36–33 Ma) primates from the Fayum deposits of northern Egypt. *Catopithecus*, an oligopithecoid from the latest Eocene horizon, has been shown to have at least a partially closed-off orbit, although it lacks symphyseal fusion and an anthropoid-like dentition. The family Parapithecidae includes species that share few features in common with living catarrhines but have a number of derived characters of their own. They may be considered either archaic members of this infraorder, little changed from its common ancestor, or more likely ancient anthropoids antedating the platyrrhine-catarrhine divergence. The Early Oligocene propliopithecids have reduced the number of their premolar teeth to the two seen in living catarrhines and have a more modern postcranial skeleton but still retain a conservative auditory region. It seems likely that they were similar to the common ancestor of the cercopithecoids and hominoids (see ANTHROPOIDEA; FAYUM; OLIGOCENE; OLIGOPITHECIDAE; PARAPITHECIDAE; PONDAUNG; PROPLIOPITHECIDAE).

Four main higher-primate groups existed in the Old World Miocene: the conservative pliopithecids of Europe and Asia, in many ways similar to the earlier propliopithecids; the African (and Asian) *Dendropithecus* and allies, which were slightly more derived postcranially; early cercopithecoids, known after ca. 19 Ma; and hominoids, first seen in the latest Oligocene, ca. 26 Ma. The third group apparently diverged from a dentally hominoid arboreal ancestor as a partially ground-dwelling lineage with a diet including more leaves and seeds than the mainly frugivorous hominoids. Although not common in the Early or Middle Miocene, Old World monkeys spread into Eurasia in the Late Miocene and possibly replaced most hominoids there as the climate deteriorated and forests shrank. The Colobinae retained conservative catarrhine facial proportions but adapted to a diet concentrating on leaves by increasing tooth relief and sharpness and developing a sacculated stomach for better digestion of cellulose. Most living species are arboreal, but two Pliocene lineages became highly terrestrial. Cercopithecines retained mainly conservative teeth and an eclectic diet but often developed elongated faces and, in a variety of lineages, a high degree of terrestriality (see CERCOPITHECIDAE; CERCOPITHECINAE; CERCOPITHECOIDEA; COLOBINAE; MIOCENE; PLIOCENE; PLIOPITHECIDAE; VICTORIAPITHECINAE).

Hominioidea

The last main group of Miocene catarrhines included the earliest members of the Hominoidea, especially the species of *Proconsul*, but perhaps also such other genera as *Kamoyapithecus* and *Rangwapithecus*. Known from 23 to 14 Ma, *Proconsul* was a quadrupedal frugivore that apparently shared a

number of derived postcranial features with later apes. The classification of the Hominoidea varies widely among authors, but here three families are recognized: one for these early African forms; a second (Hylobatidae) for the gibbons and relatives, whose ancestry is not clear; and a third (Hominoidea) for the great apes, humans, and extinct relatives. Middle and later Miocene African hominoids are relatively rare, although several new forms have recently been discovered. *Afropithecus*, *Kenyapithecus*, and probably *Otavipithecus* are among the earliest members of this clade (known between 20? and 13? Ma), grouped here in the Kenyapithecinae.

Hominoids (and pliopithecids) were able to enter Eurasia from Africa (probably via Arabia and western Asia) ca. 16 Ma, and at least four separate sublineages can be recognized until 8 Ma. *Griphopithecus*, known between 16 and 13 Ma in central Europe and Turkey, was a kenyapithecine. A more derived lineage apparently related to the living orangutan was represented in Turkey, Indo-Pakistan, and perhaps China mainly between 12 and 7 Ma. These species are commonly assigned to *Ankarapithecus* and *Sivapithecus*, although some members were previously separated as *Ramapithecus*; they share a number of facial synapomorphies with *Pongo*, but their limb bones are either more conservative or secondarily adapted to partly terrestrial life. *Gigantopithecus* was probably a very large member of this clade (Ponginae) known from a few 7 Ma specimens in Indo-Pakistan and many more from Pleistocene sites in China and Vietnam. Fossil hylobatids are also known from the latter time period onward, but it has not yet been possible to identify any older fossil as gibbonlike, because the living forms are characterized not only by generally conservative crania and dentition but also by a highly derived hominoid postcranium linked to their ricochet brachiating adaptation.

The European genus *Dryopithecus* has been known the longest, but only recently have its crania been recovered. Along with relatively modern limb elements, these remains suggest a phyletic position more derived than the kenyapithecines but without the derived orangutan features of the Ponginae. *Dryopithecus* has been found across Europe at sites estimated to date between 13 and 10 Ma, and fragmentary fossils from China and India have also been tentatively referred here. The previously enigmatic *Oreopithecus* (from a few Italian localities dated ca. 8–7 Ma) is dentally specialized but postcranially most similar to *Dryopithecus*. These two could be sister taxa, but here each is placed in a separate subfamily. The final hominid clade, Homoininae (African apes and humans), may be represented by *Graecopithecus*, known from northern and southern Greece ca. 10–8 Ma. Another member of this clade may be *Samburupithecus*, known by a single maxilla from Kenya (ca. 9.5 Ma).

The relationships among living hominoids have not been unequivocally determined from comparative morphology, but, in combination with molecular studies (especially immunology and DNA hybridization and sequencing), one phylogeny has emerged as widely acceptable. Hylobatids are seen as strongly distinct from the hominoids, implying a rather ancient divergence, although dates provided by molecular clock hypotheses are questionable. *Pongo*, the orangutan, is distinct from the African apes and humans; the subfamily

Ponginae is here recognized for the orang and its fossil relatives, as opposed to the Homininae. Views differ as to which was the first lineage to diverge among the hominines, with most molecular data placing chimpanzee closest to humans, but morphologists seeing little difference between chimpanzee and gorilla (*see* AFRICA; AFRICA, EAST; ASIA, EASTERN AND SOUTHERN; ASIA, WESTERN; BARINGO BASIN/TUGEN HILLS; DRYOPITHECINAE; EUROPE; HOMINIDAE; HOMININAE; HYLOBATIDAE; KENYAPITHECINAE; MOLECULAR ANTHROPOLOGY; MOLECULAR CLOCK; MOLECULAR "vs." MORPHOLOGICAL APPROACHES TO SYSTEMATICS; PONGINAE; PROCONSULIDAE; SAMBURUPITHECUS; SIWALIKS).

Hominini

Human evolution took place mainly in Africa in the Pliocene and the Early Pleistocene. Species of *Australopithecus*, the first-known bipedal hominine, range from ca. 4.2 to 2.2 Ma. Three species appear to more or less replace one another through this interval and may have eventually given rise to *Homo*. A collateral form may be represented by *Ardipithecus*, from deposits dated to 4.4 Ma in Ethiopia. Between 2.8 and 1.4 Ma, three species of the more "robust" *Paranthropus* are also known. Members of all of these species had large cheek teeth for their body size (means estimated at ca. 50–65 kg) and were omnivores that probably concentrated on vegetable foods. Their brains were large compared with those of great apes of similar body size, but, at 400–530 ml, they fell within the absolute size range of living-ape brains.

Significant brain-size increase is apparently evident for *Homo rudolfensis*, the earliest species placed in the same genus as living humans, and also probably the first stone-tool maker. Most fossils of this species are known from eastern Africa between 2 and 1.7 Ma, but a jaw from the Chiwondo Beds (Malawi) may date as early as 2.4 Ma, only slightly later than the oldest-known Oldowan tools, dated to ca. 2.7–2.5 Ma in Ethiopia. Another early species, *Homo habilis*, is known between 2 and 1.6 Ma in eastern and southern Africa. The earliest *Homo erectus* fossils (sometimes termed *H. ergaster*), at ca. 1.9 Ma, were apparently contemporaneous with both *H. rudolfensis* and *H. habilis*, but they differed in having a larger brain and body size, as well as cranial reorganization. By ca. 800 Ka in Europe and Africa, the fossil record yields specimens that are termed early (or archaic) *Homo sapiens* by some workers and *H. heidelbergensis* and/or *H. antecessor* by others. In turn, this group diversified into various regional sublineages or species (such as the Neanderthals in Europe and western Asia or the "Rhodesians" in sub-Saharan Africa). Eventually, anatomically modern humans evolved, probably in Africa, perhaps as long as ca. 120 Ka, developed a variety of Late Paleolithic tool kits, diverged into major geographic groups ("races"), and spread across the world displacing the other varieties by ca. 30 Ka (*see* ARDIPITHECUS RAMIDUS; AUSTRALOPITHECUS; BRAIN; HOMININI; HOMO; PALEOLITHIC; PARANTHROPUS). [E.D., I.T.]

Groves, C.P. (1989) *A Theory of Human and Primate Evolution*. Oxford: Clarendon.

Martin, R.D. (1990) *Primate Origins and Evolution*. Princeton: Princeton University Press.

Napier, J.R., and Napier, P.H. (1985) *Natural History of the Primates*. Cambridge, Mass.: MIT Press.

Shoshani, J., Groves, C.P., Simons, E.L., and Gunnell, G. (1996) Primate phylogeny: Morphological vs. molecular results. *Mol. Phylogen. Evol.* 5:102–154.

Szalay, F.S., and Delson, E. (1979) *Evolutionary History of the Primates*. New York: Academic.

Further Readings

Fleagle, J.G. (1999) *Primate Adaptation and Evolution* 2nd ed. San Diego: Academic.