PRIMATES

Primates is the order of mammals to which humans belong, together with the greater and lesser apes, the Old and New World monkeys, the tarsiers, the bushbabies, the lemurs, and various extinct groups. The relationships of the primates among the mammals have long been debated, but today Primates is most often considered to group with the orders Scandentia (tree shrews), Dermoptera (colugos or flying lemurs), and Chiroptera (bats) to form the larger grouping Archonta. Apart from the ubiquitous *Homo sapiens* (and to a lesser extent various types of macaques) all extant (modern-day) primates are tropical or subtropical, and the vast majority of species are confined to forested or wooded environments.

Definition and Classification of Primates

Arriving at a morphological definition of the order Primates always has posed a problem since it is, of course, phylogeny (evolutionary history) rather than morphology (form) that ultimately gives the group its unity. Nonetheless, if we disregard the "archaic" forms of the Paleocene, we can follow W.E. Le Gros Clark in characterizing Primates in terms of a number of "progressive trends" that marked the order's evolution. All these trends indicate the ways in which the order has diverged from other major mammalian lineages. These trends include decreased importance of olfaction (the sense of smell) and increased importance of stereoscopic vision; enhanced grasping and manipulative capacities, associated with the replacement of claws by nails that back sensitive pads on all or nearly all digits; and a tendency toward enlargement of the "higher" centers of the brain, notably the association areas of the neocortex.

Classification of the 200-odd species of primates is currently in flux and probably always will be. Partly, this is because classifications are inevitably a matter of taste, but there are also some major uncertainties about relationships within the order. The principal uncertainty concerns the tarsiers *(Tarsius)*, which have been grouped with both the "lower" primates (the lemurs, bushbabies, and lorises) and the "higher" primates (the Old and New World monkeys, apes, and humans). Scholars who adhere to the former scheme classify the living primates into two suborders: Prosimii (lemurs and relatives, plus tarsiers) and Anthropoidea (the rest). Scholars who classify the tarsiers along with the higher primates also produce two divisions: Strepsirhini (lemurs, bushbabies and lorises) and Haplorhini (tarsiers and the rest). Table 1 details these relationships.

The question is far from being resolved, but majority opinion probably rests with the second option, which we follow in the classification presented here. It is consistent with the family-level phylogeny of the primates presented in Figure 1. Because of the ongoing, active debate, we stress that this cladogram is provisional.

The Living and Subfossil "Lower" Primates

The Strepsirhini are often known as lower primates because they more closely resemble the earliest "primates of modern aspect" than do the haplorhines. In general, strepsirhinines have smaller brain-to-body weight ratios than higher primates, and more poorly developed diurnal (daytime) vision—they lack postorbital closure (a true eye socket) and have limited color vision at best. They also retain more elaborate olfactory equipment that includes a tethered upper lip (one with limited movement), and a moist rhinarium ("wet nose") that communicates with a relatively well developed vomeronasal organ (that is used to detect pheromones). This emphasis on the sense of smell is reflected in the ways in which strepsirhines communicate, which involves a great deal of scent marking though urine, feces, and exudations produced by specialized glands. Strepsirhines have abducted (well-separated) first digits and strong grasping capabilities, but compared to the higher primates, their ability to grasp with their hands is imprecise.

Strepsirhini is a diverse group, with five extant families in Madagascar and two in Africa/Asia. All strepsirhines are united by the possession of a "toilet claw" on the second pedal (foot) digit and a "tooth comb" in the lower jaw, consisting of slender, totally procumbent (horizontally projecting) front teeth. Body sizes range from about 30 to 60 grams in the tiny mouse lemurs (Microcelous) to about seven kilograms in the largest sifakas (Propithecus) and the babakoto (Indri). Until very recently (within the last one thousand years), Madagascar harbored a much wider diversity of lemurs. The larger-bodied forms apparently succumbed rapidly to the activities of late-arriving human beings. These extinct "subfossil" forms are known mostly from Holocene cave and marsh deposits throughout the island. All these forms are effectively members of the modern

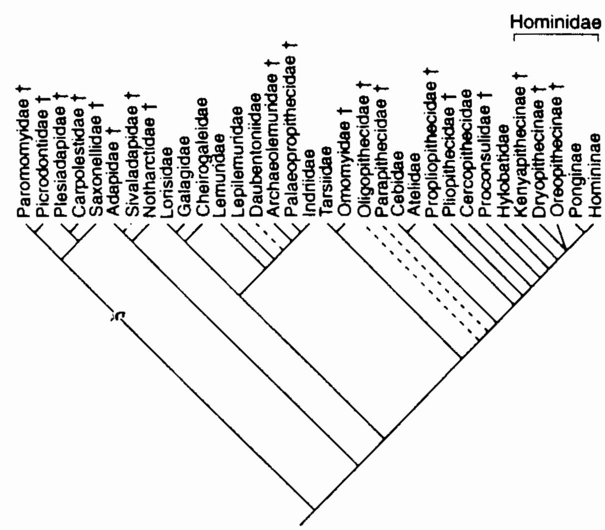

Figure 1. Consensus cladogram of primate families, with subfamilies of Hominidae. Symbols: †, extinct group; ...., probable placement of questioned taxa.

lemur fauna, so they are most appropriately considered in this section, along with their surviving relatives.

Perhaps the most remarkable of the extinct strepsirhines of Madagascar are the "sloth lemurs," family Palaeopropithecidae (Figure 2). The three smaller genera of this family show increasing suspensory adaptation with body weight (estimated to range from about 10 to 60 kilograms). Throughout the skeleton of the largest group, *Palaeopropethecus*, the joints were built for mobility rather than for stability and strength, except in the long, hooklike hands, where the tongue-in-groove phalangeal joints limited movement to a single plane and maximized power grasping. However, with an estimated weight of up to 200 kilograms, *Archaeoindris*, the largest palaeopropethecid of all, was clearly too large to have led an arboreal existence. Members of the genus almost certainly filled in Madagascar a similar niche to that occupied in the southwestern United States by the Pleistocene giant ground sloths.

Equally unusual were the species of *Megaladapis*, giant relatives (40 to 80 kilograms) of today's *Lepilemur*. Its extraordinarily long hands and feet, adapted for very strong grasping, testify that *Megaladapis* was arboreal (lived in trees), but its very short fore and hind limbs and high body weight suggest a certain lack of agility—leaping ability in particular—in this vertical clinger. This may explain its unusual skull morphology. The skull is peculiarly elongate. The foramen magnum (opening in the skull for the spinal cord) points backward, and the face is tilted up on the cranial base. These adaptations would have converted the head into a long extension of the neck, maximizing the radius within which the *Megaladapis* could crop leaves from a single sitting position. This method of eating may be reflected in the replacement of the upper incisors with a horny pad and perhaps also by the presence of a mobile snout, suggested by the heavily vascularized bone (bone with an unusually large supply of blood vessels) that overhangs the nasal aperture.

Less committed to an arboreal lifestyle were the archaeolemurids. These short-limbed, powerfully built quadrupeds had short extremities that indicate a more terrestrial way of life. These medium-bodied primates (about 15 to 25 kilograms) probably were most similar in appearance to today's baboons. One genus, *Hadropithecus*, is reminiscent of the "manual grazing" geladas in its short face, reduced front teeth, and the expansion of its cheek teeth into a formidable grinding battery.

The surviving strepsirhines of the African and Asian continents are all classified as lorisoids, with two distinctive families: Lorisidae, the slow-climbing lorises and pottos, and Galagidae, the vertical clinging and leaping bushbabies. Also included is the endemic (insular) Malagasy family Cheirogaleidae, the dwarf and mouse lemurs. All lorisoids are small-bodied (under one kilogram) and nocturnal. Although social, they are relatively nongregarious, relying heavily on scent-marking for communication between individuals.

More diverse than the lorisoids are the exclusively Malagasy lemuroids. The families Lepilemuridae (weasel lemurs) and Daubentoniidae (the aye-aye) are exclusively nocturnal, but two of the three genera are diurnal, and most of the lemuroids are cathemeral (active on a 24-hour basis). Social organization varies widely among the diurnal and cathemeral forms. Groups range from bonded pairs with immature offspring, through small, male-only and female-only groups, to large heterosexual groups of 30 or more. A few lemur species are specialized folivores (leaf eaters), and insects form a significant proportion of the diet of most of the dwarf and mouse lemurs. However, most lemur diets vary according to season and location. In general, the diurnal strepsirhines seem to be as opportunistic in the exploitation of their environments as are their "higher" primate relatives—they will eat whatever type of food is at hand.

Although tarsier-like primates were rather diverse during the Eocene, they are now restricted to four or five species of a single genus, and are found only on islands in the Philippines and Indonesia. These tiny, basically nocturnal animals live in bonded pairs and eat mainly animal protein (insects and small vertebrates). They are characterized by relatively huge eyes and eyesockets that almost fully surround the rear of the eyeball; a dry nose with a mobile upper lip; and elongate tarsal bones (ankle and rear foot bones) (hence their name) that permit them to leap large distances, often pouncing on prey. The dry nose, along with derived features of their placenta, link tarsiers to the anthropods, while the lack of a tooth comb and toilet claw separates them from the strepsirhines. Thus, they are here formally classified within the Haplorhini. Despite this classification, tarsiers, along with their extinct omomyid relatives, are best discussed with the "lower" primates as they still retain many primitive features.

The Living "Higher" Primates

Today, the major subdivision of the Haplorhini, the Anthropoidea, includes three extant superfamilies: Ateloidea (the South American—or New World—monkeys of the infraorder Platyrrhini); Cercopithecoidea (Old World monkeys); and Hominoidea (humans and apes). The latter two major taxa are combined to form an even larger group, the Catarrhini. It is important to note that the two "monkey" superfamilies are *not* each other's closest relatives—"monkey" is basically a grade-level grouping of anthropoids that are held together simply by their retention of primitive anthropoid features. Living "monkeys" are not a monophyletic group, i.e., one in which all members share a direct common ancestor.

The New World primates are in many ways the most diverse haplorhine (or even primate) clade. The smallest-bodied forms (usually under one kilogram) are the Callitrichinae (marmosets and tamarins), which live in groups of one or two pairs with offspring, often inhabiting vine tangles and low bushes. These small animals eat insects, fruit, and tree gums, and the males participate fully in infant care. Their morphology includes superficially "primitive" clawed digits and triangular upper molars. However, these features probably are evolutionary reversals rather than retained ancestral conditions.

Like callitrichines, the Cebinae (capuchin and squirrel monkeys) have a lightly built masticatory (chewing) apparatus, a mainly insectivorous diet, and a tendency to reduce the third molar (which is fully lost in marmosets). Although grouping these two subfamilies together into the family Cebidae is a relatively recent hypothesis (Rosenberger 1992) and is often questioned by other morphologists, recent molecular systematic research has, for the most part, supported it strongly.

Figure 2. Side view of skulls of *(above) Palaeopropithecus maximus* and *(below) Archaeoindris fontoynonti* (family Palaeopropithecidae). Illustration by Nicholas Amorosi.

Rosenberger's second platyrrhine family, Atelidae, is less readily characterized morphologically but is also supported by genetic studies. The large-bodied, often acrobatic Atelidae (howler and spider monkeys) have derived prehensile (grasping) tails; their robust masticatory system is suited for diets that mix fruit and leaves. Another subfamily, Pitheciinae, is more diverse, and includes the saki-uakari group *Callicebus*, and perhaps the nocturnal (or cathemeral) *Aotus*. Molecular studies often link the latter genus with cebids, but its apparently conservative features may be "confusing" this result. Pitheciines generally eat hard fruits and seeds. They have relatively robust jaws, a feature shared with atelines.

The catarrhine Old World monkeys have the most species of any primate family. Their characteristic bilophodont molars (which have two cross-ridges) and perhaps their terrestrial locomotion may be "key characters" at the root of their success. Members are widespread in Africa and eastern Asia today, while extinct relatives inhabited the circum-Mediterranean region as well. Cercopithecoids belonging to the subfamily Cercopithecinae (macaques, baboons, and their relatives) monkeys are characterized by cheek pouches for temporary food storage and relatively bunodont (low-crowned) molars. They have eclectic diets centering on fruits. The smaller-bodied guenons and mangabeys of Africa typically live in "harems" dominated by a single male, while the social organization of Asian macaques and the larger-bodied African baboons includes both large heterosexual troops of 30 to 100 individuals and one-male units that often merge into large herds of up to 500 individuals. Cercopithecoids belonging to the subfamily Colobinae (langurs and their relatives) have sharper-cusped molars with higher relief and complex sacculated (multi-chambered) stomachs. This digestive system supports foregut fermentation to break down plant cellulose, allowing a diet of both young and mature leaves. Colobine social structure also features one-male groups (often with infanticide seen during takeover by a new male), but heterosexual groups of 30 or more and even rare pair-bonded units are found in these primarily arboreal monkeys.

The Hominoidea (apes and humans) includes only five living genera, but because one of these is *Homo*, interest in their morphology and behavior has produced an immense literature. The gibbons *(Hylobates)* are usually placed in a monotypic family (i.e., only with one genus) characterized by elongate limbs and a brachiating (arm-swinging) mode of locomotion. Gibbons also have relatively conservative skulls and teeth, pair-bonded social organization, and a diet of fruit or leaves. The great apes were previously classified together in the family Pongidae, but molecular systematic studies in particular have demonstrated that the orangutan is the sister group to African apes plus humans (the Homininae). The physical characteristics of chimpanzees are most similar to gorillas, but genetic analyses place chimps closer to humans. For such a small taxonomic unit, these four genera present a great diversity of locomotor, dietary, and social patterns (even if one does not consider modern human technology).

Primate Origins and Early Evolution

The origins of the primate order are poorly documented but almost certainly extend back into the Late Cretaceous. Most of the primate fossils of the Paleocene radiation (approximately 65 to 55 million years ago) come from the northern continents, notably Europe and the western United States, but it is likely that Africa, about which very little is known before the Late Eocene, was also an early center of primate evolution. Indeed, Africa may harbor the link between the earliest primates and the later primate radiations. There has been some debate over whether the Paleocene forms (the Plesiadapiformes) properly belong in Primates. This is because these animals are both adaptively different from undoubted primates and lack any known direct links to them. Nonetheless, an exclusive shared ancestry of the Plesiadapiformes and the Primates, possibly in the late Cretaceous, is indicated quite strongly by their cheek teeth and postcranial skeletons and by aspects of the morphology of the bony ear (Figure 3).

The best-known plesiadapiform group is *Plesiadapis* (Figure 3a), found in Late Paleocene through earliest Eocene sites in both Europe and North America. Like its relatives, this animal was small-brained (compared to later primates, although not to its nonprimate mammalian contemporaries), lacked the postorbital bar that defines the outer edge of the orbit (eye opening) in all living primates, had an elongate face with enlarged and complex front teeth, and retained clawed extremities. Heavily built though they were, there is no doubt that species of *Plesiadapis* (some 15 have been recognized) were arboreal. Dental evidence suggests that *Plesiadapis* was fully herbivorous. Indeed, although the diets of the plesiadapiforms were evidently quite varied, they show a strong tendency toward lowered molar cusp relief, which suggests that there was a shift away from insect-based diets and toward diets based on plants at a very early stage of primate evolution. Abundant throughout the Paleocene, the plesiadapiforms declined as primates of modern aspect began to diversify. None survived the end of the Middle Eocene.

Evolution of the "Lower" Primates

The Eocene epoch (approximately 55 to 34 million years ago) witnessed a dramatic radiation of primates of modern aspect (semiorder Euprimates). These forms, which first arose toward the end of the Paleocene, are most abundantly known from fossils in Europe and North America. Scholars agree that these early primates, the first to resemble (in a general way) today's primates, fall into two major groups. The details of their classification are still matters of debate. One group has traditionally been aligned with Madagascar's lemurs and is assigned here to the infraorder Adapiformes of the suborder Strepsirhini. The other group's affinities have seemed to lie with the tarsiers, and accordingly the diverse Eocene superfamily Omomyoidea is classified along with the enigmatic and poorly known middle Eocene Chinese fossil *Eosimias* (Eosimiidae) in the hyporder Tarsiiformes of the suborder Haplorhini. However, it is becoming clear that this simple division obscures a more complex situation, and any classification of the Eocene primates currently remains highly tentative.

The adapiform primates lack the tooth combs and toilet claws of the strepsirhines but in many other respects are similar to Madagascar's lemurs, at least functionally. Similarly, the omomyoids possessed a recognizably modern level of organization. Eocene primates were undoubtedly arboreal, with grasping hands and feet that functioned much like those of strepsirhines. The first toe and thumb were opposed to the remaining digits, and sensitive digital pads were backed by flat nails. Braincases were relatively large and faces reduced, presumably in concordance with a decreased importance of olfaction compared to the archaic primates of the Eocene. A postorbital bar was present and, in some of the larger-eyed omomyoids, there was a certain degree of postorbital closure (i.e., a partial eye socket). This converges on the condition seen in haptorhines. The eyes were relatively forward-facing, which enhanced overlap of the visual fields and thus improved stereoscopic vision. Only a few Eocene primates had teeth that resemble those of modern strepsirhines, and it is hard to demonstrate that any known fossils of the Eocene radiations from the northern continents are the direct ancestor of any species today.

The modern groups of lower primates have sparse fossil records indeed. In the latest Eocene deposits of Egypt's Fayum, there are fossils assigned to the genus *Plesiopethecus*, whose jaws carried an enlarged daggerlike incisor. This animal has been provisionally classified as a lorisiform strepsirhine. By the Miocene epoch (approximately 24 million years ago), lorisids are more fully documented in East Africa by *Mioeuoticus* and in Pakistan by *Nycticeboides* and perhaps by *Indraloris*. The documented evolutionary history of the galagids is shorter yet, extending back to the Late Pliocene (approximately 5 million years ago) in East Africa, and only very dubiously beyond that to Miocene East African forms such as *Progalago* and *Komba.* In Madagascar the lemuriforms and the lorisiform cheirogaleids are bereft of any ancient fossil record at all, although there is a diverse late Pleistocene assemblage, along with its surviving extant members.

Early Evolution of the "Higher" Primates

The origin of the Anthropoidea has been controversial for well over a century. As more and more early primate fossils are recovered, new hypotheses of relationships to living monkeys and apes multiply. Despite earlier suggestions that platyrrhines and catarrhines might have evolved independently to "higher" primate status, modern scholars almost universally accept the idea that anthropoid primates have a single, common ancestor, probably among the tarsiiforms, typified by the Omomyidae.

In recent years, scientists have proposed a number of specific candidates for the role of earliest anthropoid. *Altiatlasius,* from the Late Paleocene of Morocco is, at best, an omomyid relative. It may, in fact, be a basal euprimate. *Eosimias,* from the Middle Eocene of China, is probably a true tarsioid, closer to the living genus than are the known omomyids. Its primitive features throw some light on the morphology of early haplorhines. A variety of other Eocene genera from Asia (including *Pondaungia* from Burma, *Siamopithecus* from Thailand, and *Hoanghonius* from China) and Africa (such as *Djebelemur* from Morocco) probably represent distinctive adapiforms unrelated to anthropoid origins. The oldest plausible anthropoid now appears to be *Algeripithecus* from the Middle Eocene (approximately 45 million years ago) of Glib Zegdou, Algeria. The few isolated molars that are known from this form are similar to those of the well-known parapithecids from the younger Egyptian Fayum sequence.

The oldest Fayum horizon, known as Quarry L-41, is latest Eocene in age. It produced the most archaic of all anthropoids, *Catopithecus,* represented by several damaged skulls and lower jaws. These present a mosaic of conservative (primitive) and derived (advanced) features. It is more primitive than later anthropoids in its dental morphology and in possessing an unfused joint between the left and right halves of the lower jaw. It aligns with later anthropoids in the loss of the interfrontal (metopic suture) of the forehead and the possession of a ringlike ectotympanic (bone that holds the eardrum) affixed to the margins of the bony middle ear opening.

In their molar morphology, *Catopithecus* and its younger relative *Oligopithecus* are significantly more primitive than *Algeripithecus.* This suggests that these Egyptian forms (collectively called oligopethecids) are little changed from basal anthropoids that lived prior to 45 million years ago. In their time, the oligopithecids were therefore "living fossils."

Oligopithecids have only two premolars, an advanced feature seen in catarrhines. This trait has prompted some workers to link them with the later propliopethecids. However, other aspects of their morphology argue against such an association.

Although present in L-41, the Fayum parapithecids are more common in the upper levels of the sequence, especially at about 33 million years ago, where *Apidium* (Figure 3e) is the most abundant small mammal. These three-premolared genera are characterized by a tendency to develop an increased number of bunodont (low, blunt) molar cusps as well as the unique presence of a central conulr (small cusp) on the upper premolars. *Apidium* has canine teeth that clearly show sexual dimorphism (males and females are physically distinct). By contrast, *Catopethecus* shows only a hint of sexual dimorphism. *Apidium* is clearly anthropoid in its fused frontal bones, fused mandibular symphysis (intermandibular joint), and possession of a fully closed orbit (eye socket). Its locomotor morphology is specialized, as it was clearly adapted to arboreal running and leaping. *Parapithecus (Simonsius),* a somewhat larger parapithecid, had lost both lower incisors, so that the two lower canines met at the symphysis (midline) of the lower jaw. Parapithecids were once thought ancestral to Old World monkeys (or at least early catarrhines), but both dental and skeletal features place them as unrelated early anthropoids, as is also true of the more conservative oligopithecids. The rare, three-premolared *Proteopithecus* from L-41 might somehow link these two families or be distantly related to the platyrrhines.

The third major group of Fayum anthropoids, on the other hand, appears to sit at or near the origin of the Catarrhini. *Propliopithecus* (including the species formerly called *Aegyptopithecus*) (Figure 3f) is known by several species from the upper Fayum horizons. Fossils of the skull and face share the derived anthropoid features noted for *Apidium,* including the conservative annular (ringlike) ectotympanic bone and a relatively small brain size. The molars are morphologically close to those of Miocene noncercopithecid catarrhines, the two premolars lack a central cuspule, and the incisors and canines are robust. Scattered postcranial remains have catarrhine-like features and indicate moderately acrobatic branch-running locomotion.

Diversification of the Modern Anthropoids

The Miocene epoch witnessed the rise of both platyrrhines and catarrhines in the southern continents. The source of the New World monkeys is still a matter of some disagreement. Once scholars realized that in the Eocene the South Atlantic was significantly narrower than today, some suggested that early African anthropoids somehow crossed to South America on rafts of floating vegetation and, once there, proliferated into platyrrhines. But no known Eocene primate is a potentially reasonable "structural ancestor" for the New World monkeys, except possibly the recently discovered Fayum *Proteopithecus.* The alternative proposal is that a North American omomyoid managed to cross the water gap across what is now Central America (perhaps via the emerging Caribbean islands). This theory implies that protoanthropoid omomyoids inhabited both eastern Asia and western North America in the Early Eocene. If one assumes omomyoid ancestry for the Anthropoidea, then this theory requires the common ancestor of platyrrhines and catarrhines to be very old, much older than the common ancestor required by an Afro-South American dispersal. The latter probably involved traveling a longer distance, but the currents were more favorable, and newly emerged islands in the mid-Atlantic may have served as stop overs. In either case, the most ancient known platyrrhine *Branisella* (which may subsume

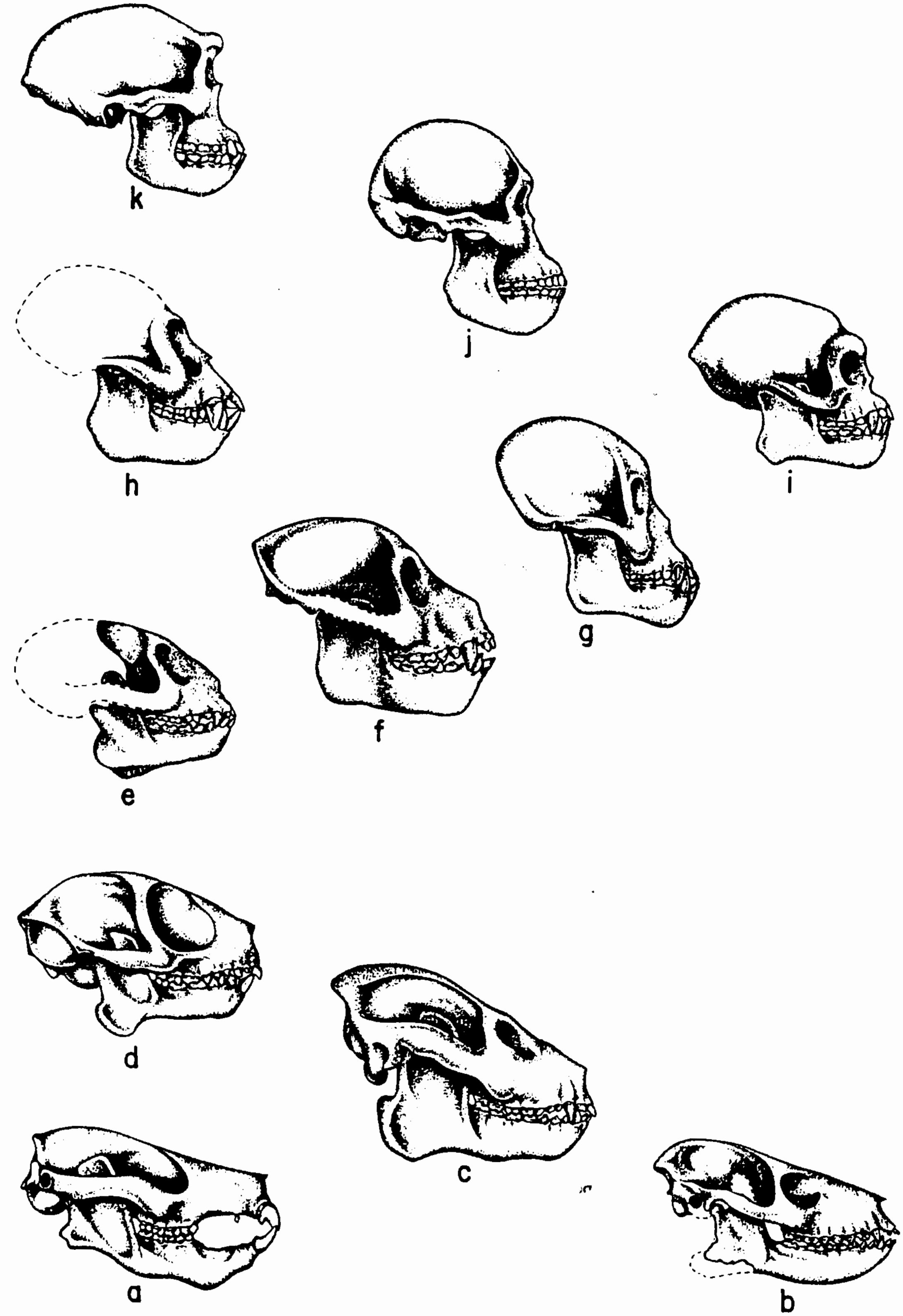

Figure 3. Side view of various extinct primates. *a*, *Plesiadapis tricuspidens* (a plesiadapiform); *b*, *Notharctus tenebrosus* (an adapid); *c*, *Leptadapis magnus* (an adapid); *d*, *Necrolemur antiquus* (an omomyid); *e*, *Apidium phiomense* (a parapithecid); *f*, *Propliopithecus (Aegyptopithecus) zeuxis* (an anthropoid); *g*, *Proconsul heseloni* (a hominid); *h*, *Cebupithecia sarmientoi* (a platyrrhine); *i*, *Pliopithecus vindobonensis* (a catarrhine); *j*, *Australopithecus africanus* (a hominid); *k*, *Homo erectus*. Not to scale. Illustration by Don McGranaghan.

the coeval genus *Szalatavus*), has been recovered only from the late Oligocene of Salla (Bolivia), approximately 27 million years ago, leaving a long time gap between it and any postulated ancestral form. That ancestor would have to be between 50 and 35 million years old, depending on which theory of dispersal is utilized. *Branisella* has been tentatively linked to one of the two platyrrhine families, Cebidae, in part because of apparent third molar reduction. This pattern of deep ancestral roots is characteristic of platyrrhines; catarrhines, on the other hand, evolve in a succession of bushlike radiations.

As recently as the late 1970s, almost all known platyrrhine fossils could be held in one's cupped hands. Intensive collecting in Argentina and Venezuela, as well as research in Chile, Bolivia, Brazil, and the Caribbean, has increased exponentially the number of fossils and taxa available for study. The new abundance has led, in turn, to a variety of conflicting hypotheses about their relationships. At least six genera are known from the Early Miocene (approximately 20 to 17 million years ago) of southern Argentina and Chile. Three of these are relatively generalized pithecines. Another is *Tremacebus*, a platyrrhine that seems to show the beginning of orbital enlargement that reaches its zenith in the living nocturnal/cathemeral *Aotus*. Two cebines round out the tally of genera. One of these, *Dolichocebus*, has a hole connecting right and left orbits (interorbital fenestra), a feature that is otherwise only found in squirrel monkeys *(Saimiri)*. An even higher concentration of taxa has been recovered from the 13-million-year-old La Venta fauna of Colombia. Among over half a dozen genera are a pitheciine close to the modern saki-uakaris, a howler-like ateline, two possible callitrichines, and species that have been tentatively included in two modern genera, *Aotus* and *Saimiri*. The Late Pleistocene caves of eastern Brazil have recently yielded partial skeletons of two atelines significantly larger than their large-bodied living relatives, while specimens from Cuba, Hispaniola, and Jamaica testify that a diverse monkey fauna lived in the Caribbean several thousand years ago or less. Although most scholars recognize distinctive atelines, pitheciines, and cebines in this assemblage, others have suggested that they all represent a unique, perhaps ancient lineage that is separate from those known today and that entered the Caribbean during the Miocene.

By contrast, few Miocene catarrhines can be linked to modern subfamilies, much less to living genera. At least four separate groups of catarrhines are known in the Early to Middle Miocene. The most archaic or conservative of these is, paradoxically, the last to appear. This "extinct living fossil" clade is the Pliopithecidae. Pliopithecids are reasonably common in Europe and China from 19 to 9 million years ago, and a few specimens are known from Pakistan and Thailand. Their teeth and postcranial skeleton resemble those of the Oligocene propliopehtecids, with wide upper molars and molar cusps that are generally arranged along the margin of each tooth. The face is short and broad, superficially resembling those of gibbons (Hylobatidae). With gibbons pliopethecids also share relatively long, gracile limbs. As a result they once were considered hylobatid ancestors. However, pliopethecids do not have any derived features that would unite them with hylobatids or any other group of hominoids. Instead, they retain many primitive catarrhine features in their postcranial skeleton and in their skull such as the presence of an only partly tubular ectotympanic. Cladistic analysis of their character states places pliopithecids just above the propliopithecids in the comblike cladogram of catarrhine taxa.

Somewhat more modern in their dentition (with more fully squared upper molars) and postcranial skeleton are several genera found in the Early and Middle Miocene of eastern Africa. *Dendropithecus* is perhaps the best known of these taxa, which do not form a monophyletic (exclusive) group but instead can be arranged as an ascending ladder of increasingly more advanced catarrhine lineages lying below the node that marks the split between the cercopithecoids and the hominoids.

Although many researchers previously held that Old World monkeys were generally more "primitive" than apes, the prevailing view today is that cercopithecids are *more* derived than hominoids, not only dentally but also in their increased commitment to terrestrial locomotion. The oldest known members of the group are represented by fragmentary jaws and teeth from northern and eastern Africa, dated between 19 and 16 million years old. From the site of Maboko Island, in Kenya's Lake Victoria, however, deposits dated between 15 and 14 million years old have produced hundreds of teeth in numerous jaws, many postcranial elements, and most recently, a nearly complete cranium of *Victoriapithecus*. Detailed analyses have shown that this primate has the bilophodont molars of modern cercopethecids, but that it also retains a small hypoconulid at the back of the first two lower molars, a cusp that is lost in all species after the Middle Miocene. Moreover, the cranium reveals an unexpected mosaic of character states: a long snout with elongate, narrow nasal bones and only moderately wide space between the eyes, rather like the cercopithecines, which were often thought more derived than the short-faced colobines. The postcranial skeleton of *Victoriapithecus* shows most of the adaptations associated with moderately terrestrial locomotion, which characterizes later cercopithecids and supports the idea that this was a basic feature of the group's origin. The diet of *Victoriapithecus* probably consisted mainly of fruit and possibly some seeds, rather than the leafy diet of colobines, whose teeth and guts are especially adapted to this monotonous fare.

Their specialized folivorous diet may have allowed colobines to spread more widely than the cercopithecines in the Late Miocene. The small *Microcolobus* is represented by a few fossils from Kenya that date to 10 million years ago. At about the same time *Mesopithecus* appears in Europe. The title of "oldest colobine" probably goes to the latter, depending upon the exact age assigned to an isolated tooth from the German site of Wissberg. The tooth's age is generally thought to be approximately 11 million years, but scholars cannot rule out the possibility that the assemblage contains fauna from a number of time periods. In many ways, *Mesopithecus* is comparable to the living hanuman langur *Semnopithecus*, with moderate terrestrial adaptations in the limbs. Dozens to hundreds of individuals are known from the Balkans, especially at Pikermi (Greece), now estimated at approximately 8.5 million years ago; the species also extended into Afghanistan. Teeth of similar size have been recovered from a 7-million-year-old site in Pakistan that lies on the other side of an important faunal barrier that existed at this time between Europe and Asia. A single *Mesopithecus*-like tooth has been recorded from a 5.5-million-year-old site in

China. Other colobine species are known in the later Late Miocene in North Africa, and the earliest cercopithecines show up there also. These are mostly represented by isolated teeth of the dentally more conservative tribe Papionini and are attributed to *Macaca*, in part because of their presence north of the Sahara. This genus apparently entered Eurasia at the very end of the Miocene, since a few teeth found in both Spain and China date from approximately 5.5 million years ago.

The Pliocene saw a strong increase in the variety of cercopithecids and their adaptive patterns. In Africa, large colobines are known across the eastern region but are rarer in the south. *Cercopithecoides* was apparently highly terrestrial, and its diet may have included a fair amount of grit, which caused heavy tooth wear (unlike ceropithecines, colobines generally do not have thick enamel to protect against such wear). The mainly arboreal *Paracolobus* (Figure 4c) may have been the largest colobine ever—up to 50 kilograms for big males. Other species, represented only by teeth, were closer to the size of living African colobines—approximately 10 kilograms for males. Papionin cercopithecines, on the other hand, may have been more diverse in South Africa, where the cave sites yielding australopiths also produce species of *Parapapio, Papio,* and *Theropithecus* (Figure 4a). Only the latter genus is common in eastern Africa, where two lineages appear to have diverged from *Papio* before 4 million years ago and from each other by 3.5 million years ago. One lineage shows an intriguingly steady increase in size through the Pliocene and well into the Middle Pleistocene, before becoming extinct. Teeth of cercopithecines appear rarely during the Pliocene and Pleistocene, indicating little more than that the group was present, probably in forests, from which there are few samples.

In Eurasia, *Mesopithecus* continued in Europe, as did a possible descendant, the larger and more terrestrial *Dolichopithecus* (Figure 4d). A few similar specimens from Mongolia and Siberia recently have been named *Parapresbytis,* but this may well be a northeastern subgenus of *Dolichopithecus.* This genus thrived in the moist forests of the southern European Early Pliocene, but by about 2.5 million years ago colobines disappeared from Europe and northern Asia. Macaques also spread widely across the continent early in the Pliocene, and several varieties in Europe may be relatives of today's living North African species. Asian forms are generally poorly known. Large terrestrial papionins occur late in the Pliocene and into the Early Pleistocene in southern Europe and Tajikistan, where they are known as *Paradolichopithecus* (Figure 4b), and in the Indian Siwaliks and China, where they are termed *Procynocephalus.* Facial differences separate these taxa, but it is possible that only one genus is actually represented; it is not certain if these populations were independent macaque derivatives or shared a unique ancestry. The Romanian population of *Paradolichopithecus* is well sampled, with males weighing up to 35 kilograms and females perhaps 20. Nonetheless, there is surprisingly low dimorphism (difference between males and females) in the cranium itself.

The Pleistocene saw the spread of modern genera of cercopithecids, after a wave of Late Pliocene extinction. Baboons and mangabeys replaced the large colobines and eventually *Theropithecus* (except for the relict population found today in the high mountains of Ethiopia), but not before some populations of the latter reached body weights of 60 to 90 kilograms. Rare specimens even document *Theropithecus* in Spain and India. A Chinese population of the large "golden monkey," *Pygathrix (Rhinopithecus),* also seems to have reached a size nearly twice that of living varieties.

Apes and Human Ancestors

For many decades, it has been dogma that the earliest generally accepted hominoid, *Proconsul* (Figure 3g), first appeared in the Miocene (approximately 22 to 15 million years ago) of eastern Africa. But in the early 1990s, Middle Miocene deposits at Lothidok (Kenya), southwest of Lake Turkana, were reassessed and found to date approximately to 26 million years ago. That pushes back the appearance of these hominoids into the Late Oligocene. Jaw fragments named *Kamoyapithecus* from this site appear to be similar to those of *Proconsul* species and can be included in the Proconsulidae. Proconsulids present a number of derived hominoid features. The skull is large and houses a somewhat expanded brain. Joint stability is enhanced by the development of a round humeral (upper arm bone) head and other postcranial modifications. The tail is absent. The upper molar teeth are broad and the molar cusp pattern is recognizably hominoid. Premolars are less heteromorphic than in more primitive catarrhines; in other words the first premolar is rather similar to the second. Proconsulids do not seem to have had much capacity for suspensory postures—they had no special adaptations for hanging below a branch. Therefore, it is postulated that they gathered fruit from a position above the branch.

The gibbon family Hylobatidae is represented in the fossil record only by later Pleistocene dental remains from China and southeast Asia. In fact, recognizing early fossil gibbons is a major problem in the study of hominoid evolution. Since their crania and teeth are relatively conservative, scholars rely on the limb bones to assess affiliation. These bones combine basal hominoid similarities (they are, however, more derived than those of proconsulids) with the elongation associated with brachiation (arm-swinging). Unfortunately, limb bones are rarely preserved. Thus, later Miocene proto-hylobatids may already have been recovered, but no derived features that could potentially link them to the modern genus have as yet been identified. Previous claims that propliopithecids, pliopithecids, or *Dendropithecus*-like forms were gibbon ancestors have been rejected because these groups have no derived features that would link them with gibbons or even hominoids.

The remaining members of Hominoidea can all be included in the family Hominidae, redefined from its earlier arrangement that included only the human lineage. The earliest hominids, the Kenyapithecinae, occur mainly in eastern Africa, but also pop up in Turkey, central Europe, and perhaps Namibia, between approximately 20 and 14 million years ago. These taxa share with later hominids relatively large upper premolars, a premaxilla (bone that holds the upper incisors) that is reoriented relative to the palate, and a somewhat more stable elbow joint. The vertebrae of the newly recognized *Morotopithecus,* dated at 20 million years old, also indicate an apelike posture, although it is not clear that this genus is truly distinct from the slightly younger *Afropithecus. Griphopithecus* appears to have been the first hominoid to exit

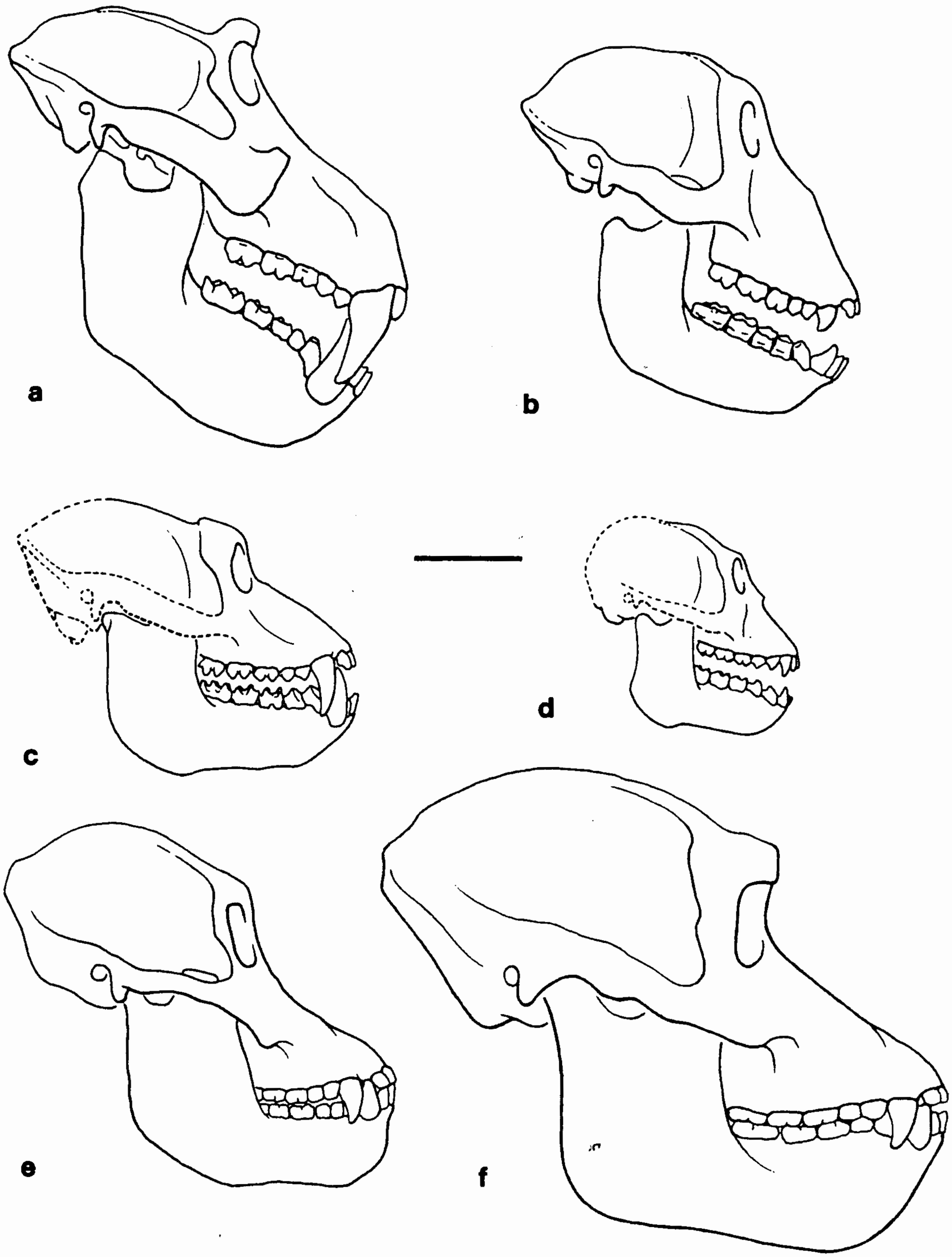

Figure 4. Side view of skulls of selected extinct catarrhines. *a*, *Theropithecus brumpti*; *b*, *Paradolichopithecus arvennensis*; *c*, *Paracolobus chemeroni*; *d*, *Dolichopithecus ruscinensis*; *e*, *Sivapithecus indicus*; *f*, *Graecopithecus freybergi*. Top row: cercopithecines; middle row: colobines; bottom row: hominids. All specimens are male except *b* and *d*. Scale: bar = 5 centimeters. Illustration by Lorraine Meeker (after Biruta Akerbergs).

Africa, dispersing from Africa through Turkey (approximately 16 to 15 million years ago) and into central Europe (approximately 16 to 14 million years ago), soon after the Afro-Arabian and Eurasian tectonic plates came into contact. Few African hominid fossils are known in the interval between 14 and 5 million years ago, during which time Eurasian taxa are better represented.

European genera such as *Dryopithecus* (approximately 14 to 10 million years ago) and the dentally unique *Oreopithecus* (approximately 8 million years ago) represent forms close to the common ancestor of the two modern hominoid subfamilies. All share further postcranial similarities with both modern groups, but no derived features characteristic of one in particular. Some scholars have suggested that *Graecopithecus* (approximately 9 to 8 million years old) displays a few specialized facial features that link it to the Homininae, but this placement is in dispute. A single maxilla (upper jaw) of similar age from the Samburu Hills of Kenya might be an African equivalent.

A more definite clade can be recognized within the Ponginae. Living orangutans *(Pongo)* have an extensive series of derived features in the face and skull: an up-tilted face with protruding incisor jaw regions set below tall, narrow, and close-set orbits and weakly projecting brows. Seen from the side, the center of the face is strongly concave, and the cheek region is expanded to the side. These features are seen in nearly modern form in *Sivapithecus* (Figure 4e), known from the Indo-Pakistani Siwalik Hills, between 12 and 8 million years ago. (Specimens previously termed *Ramapithecus* and thought to be direct human ancestors are now agreed to be female *Sivapithecus*.) A well-preserved face from 11-million-year-old Turkish deposits known as *Ankarapithecus* may represent an earlier stage in this lineage (perhaps an intermediate between *Dryopithecus* and *Sivapithecus*), despite its younger age—another "extinct living fossil."

Other potential pongines include several Chinese taxa. *Lufengpithecus* was probably a conservative dryopithecine (dating 9 to 7 million years ago). Another candidate is found in as yet incompletely published material of Mio-Pliocene Age from southwest China. Still another is the Pleistocene *Gigantopithecus*, perhaps the largest of all primates. None of these genera have the diagnostic molar wrinkling seen in living or Pleistocene fossil orangutans, and their precise relationships are uncertain.

No fossil record exists for the African great apes, *Gorilla* and *Pan*. Molecular systematic studies suggest that the human clade (hominins) had split off from proto-chimpanzees by 6 million years ago, although some researchers have argued for a significantly more recent age for this split, unreasonably implying a bipedal ancestry for *Pan*. Other than fragmentary teeth, the first probable hominin (dating approximately 4.4 million years ago) is Ethiopian *Ardipithecus*, represented by teeth with a mosaic of human-like and apelike features, a relatively forward placement of the foramen magnum (implying upright posture) and a partial skeleton whose locomotor adaptations have not yet been described.

Species of *Australopithecus* range between 4.2 and 2.3 million years old in South Africa, in Chad, and in the Rift Valley, from Tanzania through Ethiopia. These specimens preserve far more morphological detail, including crania with capacities of 400 to 500 milliliters but jaw muscles small enough that they do not require strong bony ridges for attachment sites. The teeth of these specimens include moderately large incisors, relatively small and partly incisivized (spatulate) canines, thick-enameled molars, and a broadly "humanlike" dental arch. The specimens also have a skeleton clearly adapted to upright bipedalism (supported by footprint trails), although different in detail from modern humans, with relatively short legs. Their body weight has been estimated at approximately 30 kilograms for females, up to 60 kilograms for males. Although the brain had not yet expanded to the degree seen in *Homo*, it was larger than that found in living chimpanzees of comparable size. These forms probably had an omnivorous diet, including fruits, seeds, and perhaps scavenged animal protein. There is no evidence for tool making.

The so-called robust australopiths, often placed in the genus *Paranthropus*, were generally younger (approximately 2.6 to 1.3 million years) and exhibited more specialized facial and skull anatomy. The teeth behind the canines were greatly enlarged and adapted to crushing and grinding hard food items, and (except in the earliest forms) the canines and incisors were strongly reduced. "Sagittal" (midline on top of the skull) and "nuchal" (for neck muscles at the back of the skull) crests were present to serve as attachments for the large muscles that covered the skull, and the brain was only slightly larger than that of *Australopithecus*. The postcranial skeleton is poorly known, but structure and body size were probably not much different from the earlier genus. Although some have suggested that *Paranthropus* could have made tools, there is no clear evidence of this.

Instead, the earliest tool-makers probably were species included in the living genus *Homo* (Figure 4k), first identified in deposits 2.4 to 2.2 million years old in Malawi, Kenya, and Ethiopia, soon after the oldest stone tools appeared. The exact number and interrelationships of *Homo* species is a subject of much debate, but it seems clear that early populations evolved in Africa and dispersed to eastern Eurasia between 2 and 1.5 million years ago. Continental Europe may not have been colonized until about 1 million years ago. Two major clades (each comprised of several species or subspecies) dominated the Middle Pleistocene of the western Old World. One in Europe led eventually to the Neanderthals of the last few hundred thousand years; the other, in Africa, evolved more circuitously into anatomically modern humans, some of whom dispersed via southwestern Asia to colonize the rest of the globe approximately 100,000 years ago.

IAN TATTERSALL AND ERIC DELSON

See also Hominids

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