

# A Brief Introduction to Human Evolution and Prehistory

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The study of human evolution embraces many subject areas that at first glance appear only tangentially related. Yet one cannot hope to understand our past without reference to the biotic and physical context out of which, and within which, our evolution has taken place. Thus the articles in this volume deal at least as much with questions of geology, primatology, systematics, evolutionary theory, and genetics as with the fossil and archaeological records themselves. This brief discussion is meant simply to provide a context for each of the longer entries in this encyclopedia (these are cited in CAPITAL letters), and no attempt is made to refer to every entry. For the taxonomic entries, most references are to family or larger groups. Readers will find references to relevant shorter entries (or those of lower taxonomic rank) at the end of each of the longer articles cited below. Similarly, individual genera are given a separate entry only if they are of questionable or controversial allocation, except that all extinct genera of HOMINIDAE (in the larger sense discussed below) and species of HOMININ are discussed individually.

Human beings are PRIMATES. The living primates are our closest relatives in nature, and their study enables us to breathe life into our interpretations of the rapidly improving fossil record of prehuman and early human species. The related questions as to exactly which mammals deserve to be classified as primates, and which are the closest relatives of primates, have been a matter of debate (see ARCHONTA). Under current interpretation, those extant primates that most closely resemble the early ancestors of our order are the LOWER PRIMATES of the Old World, including MADAGASCAR (see CHEIROGALEIDAE; DAUBENTONIIDAE; GALAGIDAE; INDRIIDAE; LEMURIDAE; LEMURIFORMES; LORISIDAE; PROSIMIAN; STREPSIRHINI), which are closely related to several recently extinct forms from Madagascar (see ARCHAEOLEMURIDAE; LEPILEMURIDAE; PALAEOPROPITHECIDAE) and older forms from elsewhere (see GALAGIDAE; LORISIDAE).

The enigmatic *Tarsius* (see HAPLORHINI; TARSIIDAE; TARSIFORMES) uneasily straddles the divide between these forms and the HIGHER PRIMATES, with which we ourselves are classified (see ANTHROPOIDEA; APE; HAPLORHINI; MONKEY). These latter include the New World monkeys of South America (see ATELIDAE; ATELOIDEA; CEBIDAE; PLATYRRHINI) and the Old World higher primates, or CATARRHINI, of Africa and Asia. Catarrhines embrace the Old World monkeys (see CERCOPITHECIDAE; CERCOPITHECOIDEA) as well as the greater and lesser apes (see APE; HOMINIDAE; HOMININAE; HOMINOIDEA; HYLOBATIDAE; PONGINAE).

Extant forms can be studied in a variety of ways that are useful in widening the scope of our interpretation of the fossil record. Study of the morphology of modern primates (see BONE BIOLOGY; BRAIN; MUSCULATURE; SKELETON; SKULL; TEETH) provides a base for interpretation of fossil morphology (see also ALLOMETRY; SEXUAL DIMORPHISM), as do correlated aspects of behavior (see BIOMECHANICS; DIET; EVOLUTIONARY MORPHOLOGY; FUNCTIONAL MORPHOLOGY; LOCOMOTION) and broader aspects of ecology and behavior in general (see PRIMATE ECOLOGY; PRIMATE SOCIETIES; SOCIOBIOLOGY). The traumas and developmental phenomena that occur to hard tissues during life (see PALEOPATHOLOGY) can yield valuable information about health and dietary factors in vanished populations; comparative studies of proteins and the genetic material have formed the basis not simply for hypotheses of relationship among primate and other species but also for calibrated phylogenies (see MOLECULAR ANTHROPOLOGY).

Interpretation of the fossil record clearly requires a grasp of the principles of EVOLUTION (see also EXTINCTION; GENETICS; PHYLOGENY; SPECIATION) and of the various approaches to the reconstruction of evolutionary histories and relationships (see CLADISTICS; EVOLUTIONARY SYSTEMATICS [DARWINIAN PHYLOGENETICS]; MOLECULAR "vs." MOR-

PHOLOGICAL APPROACHES TO SYSTEMATICS; NUMERICAL CLADISTICS; PALEOBIOLOGY; QUANTITATIVE METHODS; STRATOPHENETICS; SYSTEMATICS). It also requires an understanding of the processes used to name and classify living organisms (*see* CLASSIFICATION; NOMENCLATURE) and of the nature of SPECIES (*see also* SPECIATION), the basic systematic unit. Further, it is important to comprehend the nature of the FOSSIL record itself and the processes by which living organisms are transformed into fossils (*see* TAPHONOMY). This consideration brings us to the interface between PALEOANTHROPOLOGY and geology.

No fossil can be properly interpreted without reference to the geological context in which it occurs, and various aspects of geology converge on the interpretation of fossilized remains. Next to its morphology, the most important attribute of a fossil is its age. Traditionally, fossils were dated according to their relative position in the sequence of geological events (*see* TIME CHART), as reflected in their locality of discovery in local sedimentary sequences (*see* STRATIGRAPHY). Particular sedimentary strata are confined to local areas, and rocks laid down in different regions could formerly be correlated with one another only by comparing the fossil faunas they contained (*see* BIOCHRONOLOGY; LAND-MAMMAL AGES). In the past few decades, however, methods have been developed of assigning chronometric dates, in years, to certain types of rocks and young organic remains (*see* GEOCHRONOMETRY and individual dating methods). Additionally, the fact that the Earth's magnetic field changes polarity from time to time has been used, in conjunction with measurements of the remanent magnetism of iron-containing rocks, to provide an additional relative, but datable, time scale independent of fossils (*see* PALEOMAGNETISM).

The movement of the continents relative to each other (*see* PLATE TECTONICS) over the period of primate evolution has significantly affected the course of that evolution (*see* PALEOBIOGEOGRAPHY). More recently, the major geological process that has most profoundly affected human evolution has been the cyclical expansion of ice sheets in the higher latitudes (*see* GLACIATION; PLEISTOCENE) and the correlated fluctuation in sea levels worldwide (*see* CLYCIOSTRATIGRAPHY; SEA-LEVEL CHANGE). The broader relationship between CLIMATE CHANGE and EVOLUTION is also a focus of active research. A series of entries describes the geological and biological history of each continent or major geographical region (*see* AFRICA; AFRICA, EAST; AFRICA, NORTH; AFRICA, SOUTHERN; AMERICAS; ASIA, EASTERN AND SOUTHERN; ASIA, WESTERN; AUSTRALIA; EUROPE; RUSSIA).

We first find primates in the fossil record ca. 65 Ma (millions of years ago; by contrast, the abbreviation Myr is used for time spans of millions of years—e.g., in the last 65 Myr). A substantial radiation of primates of archaic aspect took place in both North America and Europe during the PALEOCENE epoch (*see* ARCHONTA; PAROMOMYOIDEA; PLESIADAPIFORMES; PLESIADAPOIDEA; PRIMATES). In the succeeding EOCENE epoch, these forms were replaced by primates more modern in aspect. Some of these, the ADAPIDAE and the NOTHARCTIDAE (combined in the ADAPIFORMES), are considered to be related in a general way to the modern lorises and lemurs; the family OMOMYIDAE, which contains

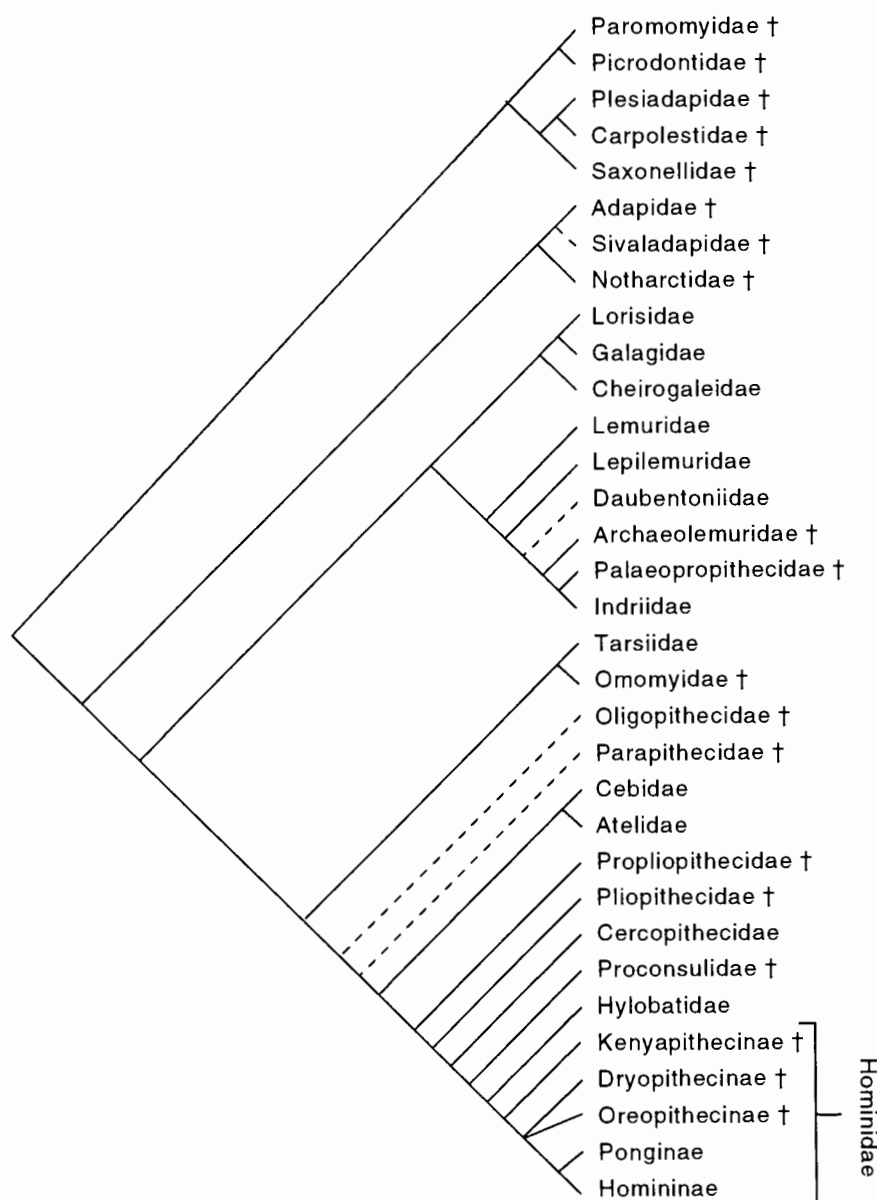
the subfamilies ANAPTOMORPHINAE, MICROCHOERINAE, and OMOMYINAE, is commonly classified within the TARSIIFORMES. Future studies may show this dichotomy among Eocene primates to be oversimplified.

At present, the higher primates, or ANTHROPOIDEA, appear to be first represented in Africa, despite claims for an Asian origin; for example, the newly discovered EOSIMIIDAE from CHINA is here included in the TARSOIDEA. Some fragmentary jaws and teeth from the Eocene of North Africa may represent early members of ANTHROPOIDEA, but the only well-represented early anthropoid fauna comes from the FAYUM of Egypt, in the Late Eocene to Early Oligocene, dating to ca. 37–33 Ma. Apart from the enigmatic OLIGOPITHECIDAE and the tarsioid AFROTARSUS, the Fayum haplorhines fall into two major groups. Of these, PROPLIOPITHECIDAE may be close to the origin of the later Old World anthropoids; PARAPITHECIDAE, although perhaps “monkey-like” in a broad sense, bears no close relationship to any extant anthropoid taxon.

The fossil record of New World monkeys goes back less far (to the latest OLIGOCENE, ca. 27 Ma) than that of the Old World higher primates, but even quite early forms generally appear to be allocable, with few exceptions (*see* BRANISELLINAE) to extant subfamilies (*see* ATELINAE; CALLITRICHINAE; CEBINAE; PITHECIINAE; PLATYRRHINI).

The MIOCENE epoch (*see also* NEOGENE) witnessed a substantial diversification of early CATARRHINI. Probably most closely affined to the propliopithecids of the Fayum was the family PLIOPITHECIDAE, a grouping of small, conservative Eurasian forms, often considered in the past to be related to the gibbons but now regarded simply as generalized early catarrhines. Their African (and Asian) contemporaries are less well understood, if somewhat more like modern forms, and are here placed in the paraphyletic “DENDROPITHECUS-GROUP.” They may have been close to the ancestry of both the apes and the cercopithecoid monkeys, representatives of which also first turn up in the Miocene (*see* CATARRHINI; CERCOPITHECIDAE; CERCOPITHECOIDEA; MONKEY; VICTORIAPITHECINAE). The cercopithecids diversified considerably during the Pliocene in Africa and Eurasia (*see* CERCOPITHECINAE; COLOBINAE).

The Miocene (and latest Oligocene) of East Africa was the scene of the first documented radiation of hominoid primates (*see* HOMINOIDEA; PROCONSULIDAE), members of the superfamily containing apes and humans. In the period following ca. 20 Ma, the diversity of hominoid species reached its peak. The first surviving subgroup of Hominoidea to branch off in this period must have been the gibbons (*see* HYLOBATIDAE), but no known form can be considered a good candidate for gibbon ancestry. The first fossil hominoids that are reasonably placed within the family HOMINIDAE are the Early to Middle Miocene (20–12 Ma) African and Eurasian genera MOROTOPITHECUS, AFROPITHECUS, KENYAPITHECUS, and GRIPHOPITHECUS, included in the subfamily KENYAPITHECINAE. Somewhat more “modern” in morphology is the European Late Miocene DRYOPITHECUS (13–10 Ma), placed in the DRYOPITHECINAE; the enigmatic European OREOPITHECUS (9–7 Ma) may also be



Cladogram showing possible relationships among the various primate families, living and extinct. This "consensus" cladogram is not intended to be a definitive statement but rather to provide a framework within which the various discussions in this volume can be understood; not all authors will agree with all the relationships hypothesized here, some of which are highly tentative. The three subfamilies of Hominae are represented separately at the far right. Daggers (†) indicate extinct taxa; dashed lines indicate especially tenuous hypotheses of relationship.

included here or in a subfamily of its own, despite past suggestions of cercopithecoïd or hominin affinities. The first extinct catarrhine genus unequivocally related to a single extant genus is the Late Miocene (ca. 12–8 Ma) SIVAPITHECUS, already close in craniodental morphology to the modern orangutan, *Pongo* (see HOMINIDAE, in this volume interpreted to include both humans and the great apes; HOMINOIDEA; PONGINAE). This extinct genus also includes *Ramapithecus*, previously considered a potential ancestor of humans. Most authorities today consider that the two African-ape genera are more closely related to humans (see HOMININAE; MOLECULAR ANTHROPOLOGY) than are the orangutan and its fossil relatives, although the question is still debated. Despite the rich Miocene hominoid fossil record of East Africa, however, no convincing precursors of the

chimpanzee or gorilla are known, with the possible exception of the gorillalike form SAMBURUPITHECUS from Kenya. The European GRAECOPITHECUS (10–8 Ma), however, is argued by some to be close to the common ancestor of Homininae and is here included in this subfamily.

A virtually complete hiatus occurs in the African hominoid fossil record between ca. 13 and 5 Ma, and subsequent to that gap the record consists of early human relatives. The earliest form that can apparently be admitted to the human CLADE is ARDIPITHECUS RAMIDUS, known by a few fragments dated to ca. 4.4 Ma. Only the LOTHAGAM mandible (ca. 5 Ma) may be an earlier member of HOMININI. More extensive collections of early human fossils are referred to species of AUSTRALOPITHECUS. The first of these is AUSTRALOPITHECUS ANAMENSIS, represented by several jaws and

postcranial elements from Kenya (ca. 4 Ma). AUSTRALOPITHECUS AFARENSIS, known from Pliocene sites in Ethiopia and Tanzania in the 4–3 Ma range, is abundantly represented by a partial skeleton and numerous other elements (see also AFAR BASIN; AFRICA, EAST; HADAR; LAETOLI; MIDDLE AWASH). Members of this species were small-bodied upright walkers (although the extent to which they had relinquished their ancestral climbing abilities is debated), as revealed not only by their anatomy but also in the trackways dated to 3.5 Ma from the site of LAETOLI. The BRAIN remained small, but the chewing TEETH were relatively large compared with body size, and the face was rather projecting. Specimens recently discovered in Chad have been given the name AUSTRALOPITHECUS BAHREIGHAZALI, although there is as yet little agreement about the distinctiveness of this form or that of the Ethiopian AUSTRALOPITHECUS GARHI.

*Australopithecus* was first discovered in South Africa in 1924, when R.A. DART described the juvenile type specimen of AUSTRALOPITHECUS AFRICANUS from the site of TAUNG. Later discoveries at the sites of STERKFORTEIN and MAKAPANSGAT provided more substantial samples of this species, which is represented between ca. 3 and 2 Ma and which differed in numerous details from *A. afarensis*. No stone tools were made at this early stage of human evolution (see AFRICA, SOUTHERN).

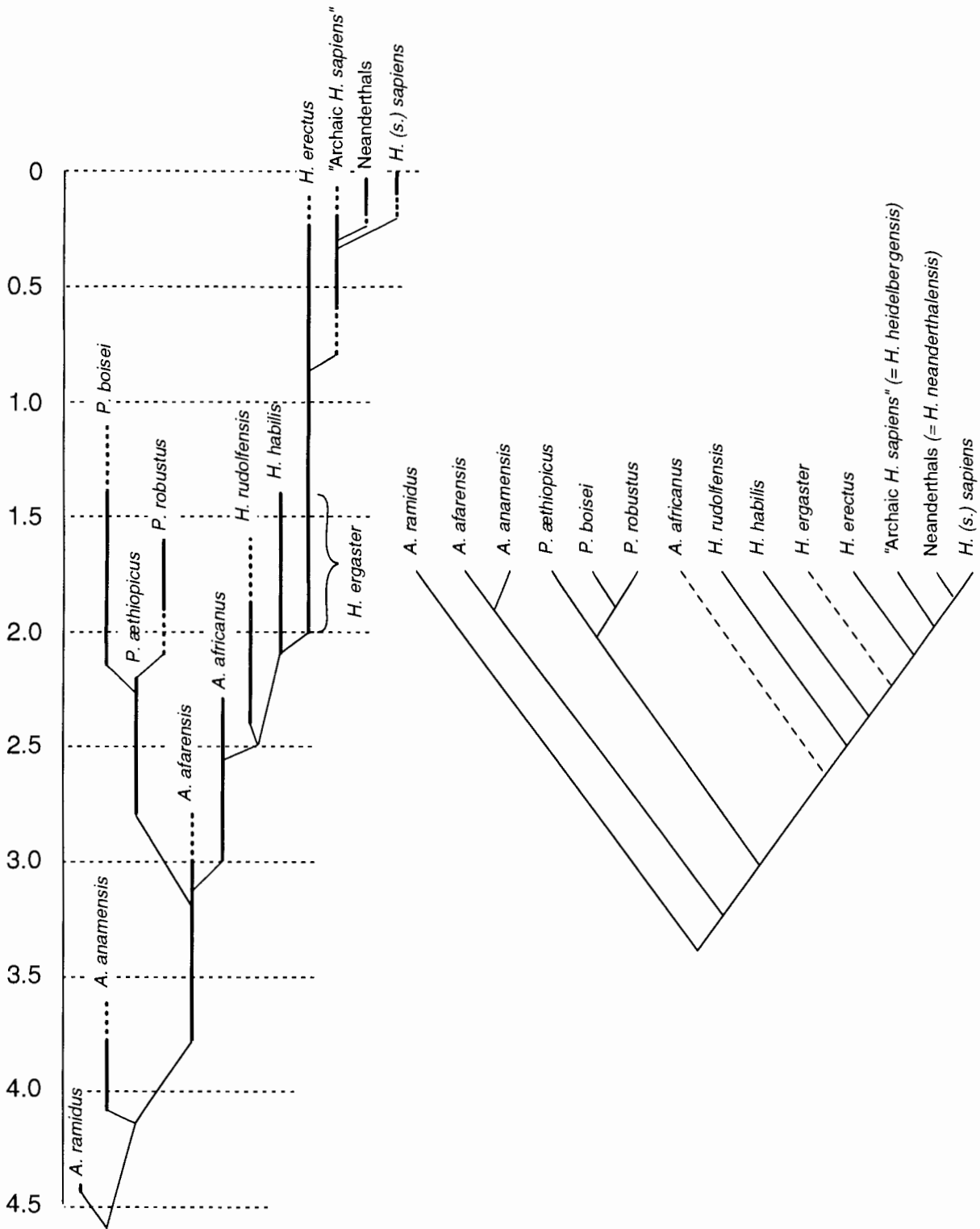
Usually, if not entirely accurately, characterized as “gracile,” or lightly built, these species of *Australopithecus* remain relatively generalized compared with the “robust” forms known as PARANTHROPUS. This genus differs from the “graciles” in numerous details of cranial architecture functionally linked to the relative expansion of the chewing teeth and diminution of the front teeth. PARANTHROPUS ROBUSTUS is known from the later South African sites of SWARTKRANS and KROMDRAAI (ca. 1.9–1.5 Ma). A related “hyperrobust” form from East Africa, PARANTHROPUS BOISEI, was first discovered by M.D. and L.S.B. LEAKEY at Tanzania’s OLDUVAI GORGE in 1959; this form, with its even larger chewing teeth and yet more diminished front teeth compared with *P. robustus*, is now well known from sites in Kenya and Ethiopia ranging from ca. 2.3 to 1.4 Ma. Less abundant material from 2.7 to 2.3 Ma in the TURKANA BASIN represents yet a third species, PARANTHROPUS AETHIOPICUS.

Although the earliest stone tools, between 2.6 and 2 Ma, are not definitely associated with any particular hominin species, it is widely believed that they were an innovation on the part of the earliest members of our own genus, HOMO. With this innovation, the archaeological record begins. Understanding STONE-TOOL MAKING and the analysis of stone-tool assemblages in terms of LITHIC USE-WEAR and the RAW MATERIALS from which they are made form only a small part of the concerns of PALEOLITHIC (Old Stone Age) archaeologists. These specialists also study the nature of ARCHAEOLOGICAL SITES, which reflect the various SITE TYPES occupied by prehistoric people. These sites are located using a number of sampling techniques, and the information they contain is analyzed through the principles of TAPHONOMY. The goal is to reconstruct the PALEOLITHIC LIFEWAYS of vanished hominins.

The earliest species allocated to HOMO is HOMO RUDOLFENSIS, mainly known from the Lake Turkana region between 2 and 1.6 Ma, but specimens perhaps belonging to this species from HADAR, Ethiopia, the BARINGO BASIN TUGEN HILLS, Kenya and URAHA, Malawi, may be as old as 2.4 Myr. The smaller HOMO HABILIS was first described from OLDUVAI GORGE in 1961, in levels dated to slightly later than 2 Ma. Fossils ascribed to *Homo habilis* have been described from Kenya, Ethiopia, and perhaps South Africa as well, in the period between ca. 2 and 1.6 Ma. Fossils allocated to these two forms were previously included in a single species, but most workers now accept a division of the diverse assemblage of specimens involved. Distinctive features of this group appear to include a more modern body skeleton than that of *Australopithecus* (although a fragmentary skeleton from Olduvai Gorge is said to show archaic limb proportions), expansion of the BRAIN relative to body size, and reduction of the face. Accompanied by an OLDOWAN stone-tool kit (see also EARLY PALEOLITHIC; STONE-TOOL MAKING), early *Homo* may have been an opportunistic HUNTER-GATHERER that killed small animals while also scavenging the carcasses of bigger ones and gathering plant foods. We have no evidence clearly demonstrating that these early humans used FIRE or constructed shelters.

Potentially the longest-lived species of our genus was HOMO ERECTUS (see also HOMO). First described from INDONESIA, *Homo erectus* is known from ca. 1.9 Ma in East Africa and persisted in CHINA up to ca. 250 Ka (thousands of years ago; also Kyr for time spans of thousands of years). The earlier African specimens are, however, often separated into their own species, HOMO ERGASTER. These first *Homo erectus* made stone tools of Oldowan type, but these were rapidly succeeded by a more complex ACHEULEAN tool kit (see EARLY PALEOLITHIC) based on large bifacially flaked artifacts, such as handaxes and cleavers, although in eastern Asia this is only rarely the case. The “Turkana Boy” early African *Homo erectus* skeleton, dated to ca. 1.6 Ma, shows that these humans were slenderly built but nearly modern in postcranial anatomy. *Homo erectus* nevertheless was highly distinctive in its cranial structure, although with a yet shorter face and larger brain than *Homo habilis* or *H. rudolfensis*. This was apparently the first form of human to learn to control FIRE (although burnt bone from SWARTKRANS at ca. 1.6 Ma might have been the work of an earlier species) and spread beyond the confines of AFRICA (see also ASIA, EASTERN AND SOUTHERN; ASIA, WESTERN; CHINA; INDONESIA), and to live in caves as well as open sites (see ARCHAEOLOGICAL SITES). It is unclear whether *Homo erectus* ever occupied EUROPE; the earliest human remains (ca. 0.8 Ma and younger) from that region of the world do not belong to this species, but have recently been called a distinct form, HOMO ANTECESSOR.

The better-known early Europeans (ca. 0.5 Ma and younger) are usually classified as belonging to an archaic form of our own species, despite strong physical differences in cranial form from ourselves (see ARCHAIC HOMO SAPIENS). These differences are striking enough to lead an increasing number of paleoanthropologists to place them in their own



Two representations of relationships in the human fossil record. On the left, a family tree showing known ranges (solid vertical bars) and possible range extensions (broken bars) of the various species recognized; light oblique lines indicate possible paths of descent. On the right, a cladogram more formally expresses hypothesized relationships among the various species. Note: *Australopithecus garhi* was named too recently to be included here.

species, *HOMO HEIDELBERGENSIS*, that is also known from other parts of the world.

Initially, stone-tool-making techniques continued more or less the same as among *Homo erectus*, but eventually a refinement was developed, leading the way to the development of the MIDDLE PALEOLITHIC stone industries. This was the

PREPARED-CORE technique, whereby a core was shaped from which a substantially completed tool could be struck with a single blow. These early humans also provide us with the first definite evidence for the construction of shelters at open sites. These were constructed using a framework of branches embedded in postholes on the ground and tied together at

the top. The same period has yielded evidence for similarly advanced humans, with cranial capacities larger than those of *Homo erectus*, in other parts of the world, including AFRICA and Asia. Their PALEOLITHIC LIFEWAYS depended on the hunting of herd animals.

Perhaps the most famous of all extinct forms of human are the NEANDERTHALS, a European and western Asian group known from ca. 200 to 30 Ka. It is their western European representatives from the latest part of this period that show the morphological specializations of the Neanderthals in the most marked degree (see also ASIA, WESTERN; EUROPE). These archaic people employed a sophisticated stone-working tradition known as the MOUSTERIAN, a variety of the MIDDLE PALEOLITHIC, and were the earliest humans to bury their dead with RITUAL practices. They were unquestionably replaced in Europe by invading waves of modern people (see HOMO SAPIENS; NEANDERTHALS), but the transition from archaic to modern human types in other parts of the world is less clear (see ARCHAIC MODERNS). A special group of entries discusses this topic from various points of view (see MODERN HUMAN ORIGINS).

All modern HOMO SAPIENS share a distinctive skull anatomy, but the origin of this physical type remains a mystery. Sub-Saharan AFRICA provides the earliest hints of ARCHAIC MODERNS (more than 100 Ka), but in all cases either the fossils are fragmentary or the dating is insecure. More recently, North Africa and southwestern Asia have yielded

remains in the 100 Ka range of individuals who were reasonably modern in appearance yet distinct from any surviving group; fully modern humans appear to have been present in eastern Asia by ca. 40 Ka also. The earliest modern humans brought with them the highly sophisticated blade-based stone-working industries of the LATE PALEOLITHIC (see also STONE-TOOL MAKING). This phase is most clearly documented in EUROPE, where it is termed the UPPER PALEOLITHIC and is accompanied by the earliest evidence for art, notation, music, and elaborate body ornamentation (see CLOTHING; PALEOLITHIC IMAGE; PALEOLITHIC LIFEWAYS; RITUAL). It was modern humans, too, who for the first time crossed into the New World (see AMERICAS; PALEOINDIAN) and traversed a substantial sea barrier to reach AUSTRALIA, where a series of highly interesting paleoanthropological finds has been made.

Following the end of the most recent glacial episode, ca. 10 Ka, the big-game-hunting cultures of the European UPPER PALEOLITHIC waned, yielding to the differently adapted societies of the MESOLITHIC period. It was perhaps first in the "Fertile Crescent" of southwest Asia that the next major economic and social developments occurred, with the growth in the NEOLITHIC period (New Stone Age) of settled village life and the DOMESTICATION of animals and plants. These developments paved the way toward COMPLEX SOCIETIES and the written word, and hence toward the end of the long period of human PREHISTORY.

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*Second edition*

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