HUMAN EVOLUTION: A PALEOANTHROPOLOGICAL PERSPECTIVE

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Keywords: Human evolution, Miocene apes, *Sahelanthropus*, australopithecines, *Australopithecus afarensis*, cladogenesis, robust australopithecines, early *Homo*, *Homo erectus*, *Homo heidelbergensis*, *Australopithecus africanus/Australopithecus garhi*, mitochondrial DNA, homology, Neandertals, modern human origins, African Transitional Group.

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Summary

The basic course of human biological history is well represented by the existing fossil record, although there is considerable debate on the details of that history. This review details both what is firmly understood (first echelon issues) and what is contentious concerning human evolution. Most of the contention actually concerns the details (second echelon issues) of human evolution rather than the fundamental issues. For example, both anatomical and molecular evidence on living (extant) hominoids (apes and humans) suggests the close relationship of African great apes and humans (hominins). That relationship is demonstrated by the existing hominoid fossil record, including that of early hominins. The fossil record also records the initial radiation of early hominins in Africa, the origin of the genus *Homo*, the spread of hominins out of Africa, the regional diversification of *Homo*, the emergence of Neandertals and other archaic pre-modern hominins, and the origin of modern people. This review details these basic aspects of human biological history and also discusses the major controversies and the theoretical differences that underlie different perspectives. Particular attention is paid to discussing the morphological characteristics that are important in interpreting fossils and how those characteristics are viewed by different theoretical perspectives. Major controversies discussed are: the hominin status of African hominid fossils dating between about 7 and 4.4 ma (million years ago); details of the phylogeny of the australopithecines, particularly the robust australopithecines; the origin of the genus *Homo*, and the origin of modern humans. The major theoretical models suggested to explain the major events in human evolution are also discussed.

1. Introduction

Scientific knowledge concerning the biological history of humans is based on extensive amounts of data taken from numerous scholarly disciplines. Some of these data are derived from the classic application of comparative anatomical analysis to humans and their closest relatives in the biological order Primates (particularly in the superfamily Hominioidea, which comprises all living and fossil apes, including humans). In addition, comparative genetic data on the Hominoidea (hominoids) have also played a significant role in the current understanding of human phylogeny, in some cases corroborating the data from anatomy and in other cases presenting somewhat different patterns. Genetic data have even been extracted from some fossil human remains, but these are quite late and are only relevant to the issue of the origin of modern people. Also the last half-century has witnessed major developments in the establishment of more accurate chronological frameworks, judicious use of models based on selected non-human primates and recent human populations to understand earlier human population dynamics, interpretation of archaeological data in the context of human biological evolution, and ability to extract better paleoecological information from pertinent fossil-bearing deposits. However, despite the importance of all this information, the most important data relevant to understanding the course of human evolutionary history is the most direct evidence we have of that history: the human fossil record. Though data from other sources will be used in supporting roles, this essay focuses on human evolution as demonstrated by the fossil record.

2. Reconstructing Biological History: The Relationship of Humans and Apes

Patterns of biological relationships are reflected in the shared possession of homologies among organisms. Homologies are similarities in structures that are derived from common ancestry and can be identified through either anatomical or molecular biological (genetic) analyses. A series of molecular studies over the last few decades has conclusively demonstrated that humans and apes are more similar to each other genetically than any of them is to any other organism (including other Primates). These molecular data confirm a conclusion long held on the basis of anatomical structures: humans and apes are part of the same evolutionary clade, distinct from other such clades. This closeness in terms of biological history is reflected in the classification of all apes and humans in the same superfamily, the Hominoidea. However, the genetic data have provided some surprises as well. Traditionally, hominoids have been divided into three families: Hylobatidae (lesser apes – the gibbons and siamangs), Pongidae (great apes – orangutans, gorillas, chimpanzees, and bonobos), and Hominidae (humans) largely on the basis of anatomical distinctions. However, the molecular data

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demonstrate that the traditional family level division of Hominidae (human) from Pongidae (great ape) is no longer appropriate, because humans and African great apes (gorillas, chimpanzees, and bonobos) form a closer group genetically than do African and Asian great apes. While there are other ways to deal with this taxonomically, what seems to be the most appropriate taxonomy is presented in Table 1. The major changes, compared to the traditional taxonomy, are that: (1) all great apes are now included in the family Hominidae (traditionally the family reserved for humans), (2) the family "Pongidae" is invalid, (3) orangutans and their specific ancestors are classified in the subfamily Ponginae of the Hominidae, (4) the extant African great apes and humans are classified in the subfamily Homininae of the Hominidae, and (5) gorillas, chimpanzees/bonobos, and humans and their specific ancestors are placed in separate tribes of the Homininae: Gorillini, Panini, and Hominini respectively. Thus the term hominin refers to extant and fossil humans; hominine refers to members of the African ape/human clade; hominid refers to members of the great ape/human clade; and hominoid retains its traditional meaning. This classification will be used in this chapter.

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Family	**Subfamily**	**Tribe**	**Genus**
Proconsulidae			Proconsul
			Kamoyapithecus
			Rangwapithecus
Hylobatidae			Hylobates
Hominidae	Kenyapithecinae		Afropithecus
			Morotopithecus
			Kenyapithecus
			Otavipithecus
	Oreopithecinae		Oreopithecus
	Dryopithecinae		Dryopithecus
	Ponginae		Pongo*
			Sivapithecus
			Ankarapithecus
			Gigantopithecus(?)
	Hominae	Panini	Pan*
		Gorillini	Gorilla*
			Samburupithecus(?)
		Hominini	Homo*
			Sahelanthropus(?)
			Orrorin (?)
			Ardipithecus
			Kenyanthropus(#)
			Australopithecus
			Paranthropus(#)

Table 1. Classification of the superfamily Hominoidea (order Primates). Note that only selected fossil genera are included. Genera marked with an asterisk (*) are genera with extant species. A question mark (?) indicates uncertain placement, and a (#) indicates genera that have uncertain validity.

On cursory examination, the anatomical similarity that defines the hominoids as a uniquely related group may not appear obvious, due mainly to the rather unique course of human evolution since their split from other hominoids. Extant humans exhibit a series of anatomical features relating to their development of obligate bipedalism, extensive degree of encephalization, and loss of ape-like characters in the dentition (canine complex) and face that gives them a distinctive appearance compared to other hominoids. However, there is a suite of somewhat less obvious anatomical homologies that reveals the close biological relatedness of all hominoids and justifies their placement in a common subfamily. For example, all hominoids have a pectoral girdle in which the scapulae are place at the lateral rear of a relatively broad thorax, a comparatively elongated clavicle, a rounded humeral head, and a trapezius muscle that attaches to the clavicle. These features all relate to enhanced mobility of the shoulder/upper limb in hominoids which underlies their suspensory locomotor pattern. Also the wrist is adapted for mobility, for example in the reduced ulnar styloid process. On the other hand, some parts of the hominoid body are adapted to greater stability. These include the elbow and the lower back, in which the number of lumbar vertebrae is reduced and their form is altered to stabilize the back. Hominoids also lack external tails, but rudimentary caudal vertebrae remain. There are other features, but perhaps the most distinctive unique defining homology of hominoids is the form of their mandibular molars. Hominoids all exhibit a pattern on the occlusal surface of their molars termed the “Dryopithecine” or Y-5 pattern. Basically the cusps and fissures of these molars are arranged so that the five (often four) cusps are separated by fissures that form a Y pattern (or an X or + depending on which cusps are in contact). No other organisms exhibit this molar pattern, or the complex of other features that have been identified as distinctive for hominoids. But apes and humans, both fossil and extant forms, do. Thus from a biological standpoint, the Hominoidea is a clearly defined group, and humans are unquestionably hominoids. This means we are unequivocally a branch of the ape family tree, albeit a highly modified twig.

Based on this complex of features, it is possible to generally outline the origin and pattern of evolution within the Hominoidea, although many details are not totally clear. Both the molecular and morphological data provide strong evidence that hominoids should have a monophyletic origin distinct to the superfamily. From a scientific perspective, the human-ape connection and the monophyly of hominoids can be established as a hypothesis, and the test of this hypothesis rests on the pertinent fossil record. The earliest group of animals that exhibit a combination of some of the defining hominoid features is the genus *Proconsul*, found in East Africa during the first half of the Miocene. There are four or five species of proconsuls that span the time range from ~23 – 14 million years ago (ma), but a related form (*Kamoyapithecus*) extends back to 26 ma. In body size they range from ~8 to 90 kg, basically from the size of a gibbon to that of a female gorilla or male chimpanzee. The proconsuls have the hominoid molar pattern, lack a tail, exhibit hominoid features of stability in most joints, and have an overall cranial and dental anatomy like living apes. However, they are primitive compared to most hominoids in that they seem to be generalized quadrupeds lacking the adaptations for mobility that characterize hominoids. The genera *Proconsul* and *Kamoyapithecus*, possibly along with a few other genera, are classified in the family Proconsulidae (see Table 1); and this family, on the basis of its morphological pattern, can be viewed as incipient hominoids. There is some debate as to whether the

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proconsuls could be the actual basal hominoid stock, but even if they are not, that basal stock would have had to be very much like them. Additionally, a 26-28 ma origin of hominoids would make sense in the light of molecular evidence, rendering the proconsuls good candidates for representatives of the incipient hominoid radiation. This and the other information discussed shortly add strong credence to the idea of a monophyletic origin for hominoids.

By 20 ma, some African apes appear to have developed more typically hominoid body form. The genus *Morotopithecus* from Uganda is poorly known but apparently had developed many of the joint mobility features and the lumbar vertebral anatomy characteristic of extant hominoids. Later African genera (17-14 ma), such as *Afropithecus* and *Kenyapithecus*, show some similarities to African great apes, but this is not based on the presence of any shared derived homologies between them and hominines. These forms apparently postdate the divergence of the lesser apes (family Hylobatidae) from the great ape clade but not the division between hominines and pongines (see Table 1). At ~17 ma, a permanent land contact is established between Africa (including the Arabian Peninsula) and Asia, providing the first opportunity for apes to spread from their natal continent into Eurasia. Several hominid genera appear in the Eurasian record after 17 ma, including the European genera *Dryopithecus* and *Graecopithecus*, and the Asian genera *Ankarapithecus*, *Sivapithecus*, and *Gigantopithecus.* At its height, the Miocene ape radiation covered most of Africa and a wide belt of forested areas from Spain to China and was represented by some 20 hominoid genera.

Some Asian genera, particularly *Sivapithecus,* appear to share some derived homologies with orangutans, particularly in the skull and teeth. Among these are an Asian subnasal pattern, narrow interorbital area, concave lateral facial profile, and complexly wrinkled occlusal enamel on the molars. *Sivapithecus* is considered to be less derived than *Pongo*, but the genus is clearly a part of the orangutan (pongine) clade. *Sivapithecus* is found in the Siwalik Hills of India and Pakistan from ~ 12.5 to 8 ma, and a morphologically similar genus, *Ankarapithecus,* comes from Turkey at ~ 10 ma. Molecular studies indicate that the Asian/ African clade split occurred between 16 and 10 ma, and the chronology and morphology of *Sivapithecus* and *Ankarapithecus* are consistent with the molecular divergence data. A possibly related genus, *Gigantopithecus,* is probably the largest ape to have ever lived, and its presence in China at 400 000 years ago (400 ka) makes it one of the latest surviving extinct apes known.

The European genus *Dryopithecus* is distributed in several species from Spain to Georgia and ranges in age from ~13 to 8 ma. Cranial features, including the subnasal morphology and facial form indicate membership in the African great ape (hominine) clade. But in reality, the hominine clade is not easy to define precisely, because it is characterized by few derived homologies. The subnasal and cranial patterns (broad interorbital, straight or convex lateral facial profile) appear to be primitive retentions, and many of the derived features hominines exhibit do not preserve in fossils. Postcranial anatomy suggests a body form similar to extant hominids, but in some ways *Dyopithecus* is seen as intermediate between modern and more primitive apes. The mosaic of morphology has lead to the classification of *Dryopithecus* and related forms in a separate subfamily, the Dryopithecinae, but similarity to the Homininae has led to

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the suggestion that the hominine clade may have evolved in Europe, in the form of a drypothecine, and migrated back to Africa. At the current time, however, the area of origin of the African great ape clade is not determinable.

The ape fossil record in Africa itself after about 14 ma is sparse. It is tempting to think that some of the apes living between ~17 and 14 ma in Africa might be members or precursors of the African ape clade, but aspects of their morphology are too primitive to make a strong claim. The same is true for the gracile *Otavipithecus* mandible, the only fossil ape known from southern Africa (Namibia) dated to ~12 ma. The only somewhat convincing fossil member of the hominine clade in Africa during the period from 17 to 7 ma is a partial 9.5 ma maxilla from Kenya assigned to its own genus, *Samburupithecus.* The upper premolar and molar form in this specimen is similar to the condition in gorillas, and *Samburupithecus* is often considered a gorilla ancestor. Despite the sparseness of the record, the African ape clade is certain to have derived from the stock represented by the non-pongine hominid forms discussed above. This is based in large part on molecular and anatomical data from living hominids, but it is also supported by the morphology of the earliest members, or possible members, of the human (hominin) clade. Thus the morphological pattern of the earliest hominins provides solid support for the hypothesis that hominins are derived from the African ape lineage.

3. The Human Fossil Record: Basal Hominins

The genus *Australopithecus* was used for the earliest hominins for most of the last half of the twentieth century. From 1978 until a decade ago, the taxon *Austalopithecus afarensis* was generally considered the most primitive known hominin and the root of subsequent human evolution. The primitive morphological pattern of *A. afarensis* compared to later hominins is well documented, representing as it does a mosaic of ape features combined with ape-reminiscent, general hominin and specifically australopithecine characters. However, beginning with the 1994 recovery of fragmentary fossils from Aramis in the Middle Awash of Ethiopia, a series of possible hominins have been found that date earlier than *A. afarensis* and are more primitive—meaning more ape like. The question for these remains is whether they are representatives of the hominin or another hominine clade. Unfortunately most of these finds are either a collection of relatively fragmentary pieces or a single specimen, and many are distorted in some significant way.

The earliest-dated potential hominin comes from the one region of Africa to yield early hominins that is not associated with the East African rift valley system or in South Africa. At the locality of Toumai in north central Chad, a single skull and a half mandible were recovered in 2001. Based on a biostratigraphic correlation to the Namata Formation at Lothagam, these specimens are estimated to date between 6.4 ma and 7.5 ma. An age anywhere in this range would make these two specimens, assigned to the taxon *Sahelanthropus tchadensis*, the oldest members of the hominin clade known to date. Several features are claimed to demonstrate *Sahelanthropus'* hominin status, including: presence of a small canine with apical wear (unlike apes), a relatively orthognathic face, a more horizontal orientation of the nuchal plane, and a more centrally located foramen magnum. On the other hand, the skull has a very small cranial

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capacity (320-380 cm^3) which is chimpanzee or bonobo sized and much smaller than any australopithecine. The small brain, as well as a pronounced supraorbital torus, evidence for distal wear on the canine, a flat mandibular fossa and a compound nuchal crest, has lead to claims that *Sahelanthropus* might represent an ape rather than a hominin. Since its age is similar to the molecular biological estimate of 5-8 ma for the African ape/hominin split, it might well be that the mosaic of features *Sahelanthropus* exhibits is to be expected for a very early hominin, but the problem is the same morphology might be expected for a form in the line before the split or from a closely related non-hominin clade after the split. Yet another problem is that the skull is markedly distorted and the maxillary canine is broken, both of which make it difficult to be certain what the real morphology of the specimen is. Thus, some degree of uncertainly will surround *Sahelanthropus* until additional specimens are found.

From the Lukeino Formation in northern Kenya, a series of fragmentary hominine remains are dated to 5.6 to 6.2 ma and include the “Lukeino molar” (a lower first or second molar that is similar to both other possible early hominins and chimpanzees). In 2000, analyses of several teeth, cranial fragments, and some postcranial remains led to the classification of this material into a new taxon, *Orrorin tugenensis*, and the interpretation that this taxon definitely represented a hominin. The strongest argument is based on two femora which exhibit bipedal features in external anatomy (e.g. a medial position of the lesser trochanter, position of the gluteal line and other head/neck features) and internal structure. Other features suggested to link *Orrorin* to hominins include thick occlusal enamel on molars, broad upper central incisor, and an apparently relatively thick mandibular corpus. While these features certainly characterize early hominins, all but the last feature are found in apes as well. An upper canine is large but not strongly projecting. It may also have remnants of a distal cutting blade. Like the other specimens, this canine has a morphology that might align it with other early hominins but cannot totally exclude it from apes, particularly the morphology in females.

The genus *Ardipithecus* has been defined on the basis of two Ethiopian sites: Aramis, dated to 4.4 ma, and the earlier Kadabba (5.2 to 5.8 ma). Most of the samples from both sites comprise fragmentary remains and individual teeth, but there is apparently a yet undescribed partial skeleton. The fauna indicates a forested environment at Aramis, an ecological setting that differs from later early hominin sites. A cranial base fragment from Aramis may have a more anterior placement of the foramen magnum, but this is not certain. The mastoid region of the fragment is highly pneumanized and the mandibular fossa flat—features characteristic of apes but also found in definite early hominins. Other potentially early hominin features include a maxillary canine that is large but more incisiform than is common in apes, but the sectorial form of the mandibular third premolar and the ape-like form of the first lower deciduous molar are more primitive than definite early hominins. Also unlike most other fossil hominids from the late Miocene/early Pliocene, molars are relatively small with thin occlusal anatomy. The latter feature, which is more like extant African apes than early hominins, is possibly an aspect of *Ardipithecus’* forest adaptation. The morphology of the partial skeleton, when published, should clarify whether this genus represents the hominin or another closely-related hominine clade.

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Although there are a few other fragmentary specimens that predate ~ 4.5 ma, the two remaining significant pieces are both small mandible fragments from the sites of Lothagam and Tabarin, both from Kenya and dating from 5 to 5.8 ma. Both are fragments of posterior mandibular bodies with one (Lothagam) or two (Tabarin) molars preserved. The teeth are like those of the australopithecines in shape and have thick occlusal enamel. The mandibular corpus of Lothagam has close similarity with *Pan* but seems to reflect a shorter face like early hominins. These specimens may well be early hominins, but the fact that they are only small fragments makes a certain attribution to the human clade untenable. In fact, essentially the same issue pervades the assessment of all these potential Miocene/early Pliocene hominins. Although each of the specimens/samples discussed above could be hominins, there are uncertainties associated with each that only the recovery of additional specimens will resolve. At the very least, these specimens ranging from ~7 to 4.4 ma provide a concrete demonstration that hominines are present in Africa during this period. For each of the examples a case can be made for hominin affinities, which, if true for all of them, would almost double the time depth of the human lineage. In either case, these remains demonstrate the difficulties to be faced in unequivocally recognizing the beginnings of that lineage.

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Biographical Sketch

Fred H. Smith is a human paleontologist with specific interests in the paleobiology of Neandertals and the origin of modern humans. He has analyzed pertinent fossil human material throughout Europe, western Asia, and Africa but has focused most of his efforts on late Pleistocene human remains from Central Europe. Smith has worked for more than 30 years on the Neandertal samples from Vindija and Krapina in Croatia and early modern human specimens from throughout the region. He is the author of over 100 scholarly publications on human evolution, and his book *The Origins of Modern Humans: A World Survey of the Fossil Evidence*, co-edited with Frank Spencer, was named the outstanding book in the life sciences by the American Association of Publishers in 1984. Smith has been a visiting professor at the Universities of Hamburg and Tübingen in Germany and the University of Zagreb in Croatia. In addition to several university level awards for teaching and research, he has been an Alexander von Humboldt Fellow in Germany, a National Academy of Sciences Exchange Scholar in the Czech Republic and Croatia, and a Fulbright Fellow in Croatia. Smith previously taught at the University of Tennessee and Northern Illinois University and is currently professor and chair of the new Department of Anthropology at Loyola University in Chicago. He also serves on the Board of Directors and as Chair of the Scientific Advisory Committee of the Midwest Museum of Natural History in his hometown of Sycamore, Illinois.