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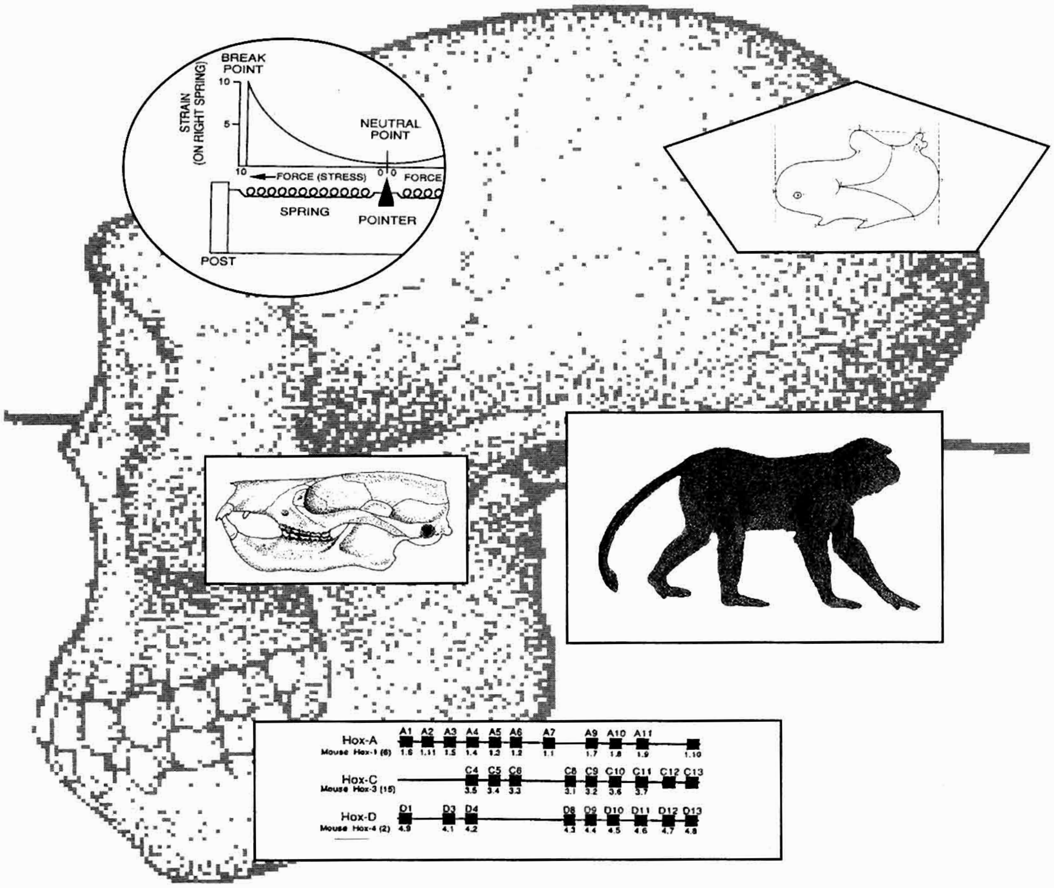

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CALIBRATION AND EXTENSION OF THE RECORD OF PLIO-PLEISTOCENE HOMINIDAE

Noel T. Boaz

ABSTRACT

Paleoanthropological research centered in the Pliocene (1.8 - 5.0 ma) and Pleistocene (10 ka - 1.8 ma) Epochs continues as one of the most active areas of biological anthropology. New discoveries have extended the sample of fossil hominids, their geographic extent, and their temporal range in virtually all parts of the world. Particularly significant are discoveries of new early African hominid taxa, *Ardipithecus ramidus* and *Australopithecus anamensis*, the recognition of an early australopithecine in Chad some 2,500 km west of the African Rift Valley, new dating results that indicate that Java, China, and the Georgian Republic contain early *Homo* fossils nearly as old as the earliest members of the genus in Africa, the recovery in England of a 400,000-year-old tibia of archaic *Homo*, and research that shows that anatomically modern *Homo sapiens* appeared in the Middle East almost as early as these populations are seen in Africa. Paleoenvironmental change is playing a greater role in interpretations of hominid evolutionary events, and taxonomic splitting of early hominid species is on the rise. Debates that are current are the "Out-of-Africa" vs. the Multiregional Model of modern *Homo sapiens* evolution and how molecular analyses relate to these questions; the taxonomic statuses of earliest *Homo* and *Homo erectus*, and consequent phylogenetic implications; paleoclimatic forcing and punctuated equilibrium in the hominid fossil record; and the selective forces and timing of human brain evolution, arborealism, tool use, scavenging, cannibalism, and fire use. Research and debate are played out on the field of three shifting paradigms: Culture, Evolutionary Biology, and Human Paleontology. The field has, moreover, become fully interdisciplinary, adding molecular biology, geophysics, and ecology to its core disciplines. There are important paleoanthropological research questions from the pre-australopithecine part of the record in the early Pliocene up to *Homo sapiens* evolution in the late Pleistocene.

KEY WORDS:

Hominidae, *Australopithecus, Homo habilis, Homo erectus, Homo sapiens,* Pliocene, Pleistocene, Evolution

THEORETICAL PERSPECTIVES

There are three explanatory frameworks or paradigms which have buffeted paleoanthropology during the twentieth century. The first is the cultural paradigm, which is the idea that human beings have adapted to, live within, and evolve through a learned system of patterned behavior that is passed on socially. This paradigm owes much of its definition to Franz Boas and it is that on which the American academic anthropology department is based. Some of the major assumptions of this paradigm have begun to unravel as the unitary nature of culture has come into question (but see Kelso, this volume). Boasian anthropologists, such as Alfred Kroeber, could assume that "culture" was a defining characteristic of Hominidae and that a sharp point of division separated "man" from "animal" or "ape." But discoveries in primatology, such as Jane Goodall's observations at Gombe, as well as in the archaeological record (Isaac, 1978) showed that culture probably did not appear at a "critical point" as Kroeber and others had postulated. Instead, there has been a long, slow evolution from various forms of early and not fully formed varieties of culture. In this paradigm behavioral change in human evolution is ascribed primarily to cultural change, although at the earliest phases of human evolution morphological differences from modern *Homo sapiens* were clearly significant. Nevertheless, most paleoanthropologists in this paradigm would suggest that hominid *capacities* for behavior, not the behaviors themselves, have evolved. Paleoanthropologists who work within the cultural paradigm are primarily archaeologists; they might be members of the newly organized Paleoanthropology Society, the Society of Africanist Archaeologists, or the Society of American Archaeology. They publish in the general anthropological journals, such as *American Anthropologist*, *Current Anthropology*, and *Man*, and in archaeological journals.

The second paradigm is the evolutionary biology paradigm and it is based on the modern synthetic theory of evolution by natural selection. The origins of the association between this "natural history" approach and anthropology go back to the beginnings of the discipline, during the Enlightenment (Blumenbach, 1776). The Neo-Darwinian Synthesis states that all living systems compete for resources because basic principles of individual variation, genetic inheritance, population increase, and limited environmental resources will cause some individuals to reproduce more effectively than others. Human evolution in this view is seen as a series of past populations evolving just the same as other biological species. Genetics and molecular evolution are embraced by one set of paleoanthropologists who have adopted this paradigm. Adherents to this school tend to ascribe importance to understanding natural variation within populations, to be taxonomic lumpers, to interpret anatomy of fossils within a "total morphological pattern" (Le Gros Clark, 1964), and to be interested in "horizontal" problems, i.e. questions of paleoecology and behavior at particular time planes in the past, in addition to "vertical" problems of hominid phylogeny. Evolutionary-biology-paradigm paleoanthropologists in general accept the ethological notion that behavior evolves and with that acceptance they tend to believe in a greater degree of genetically based behavior in human evolution than do the cultural-paradigm paleoanthropologists. These paleoanthropologists are generally members of the American Association of Physical Anthropologists and frequently publish in the *American Journal of Physical Anthropology*, general science journals such as *Nature* and *Science*, and in such specialty journals as *Journal of Human Evolution*, *Human Evolution*, and the new *Evolutionary Anthropology*.

A third paradigm within paleoanthropology is the human paleontology paradigm. It is related to the second paradigm but it has some differences. Human paleontology has a venerable history extending back to the Neander Valley and beyond, but until recently it has tended to be simply the methodological handmaiden of anatomy or evolutionary physical anthropology. This changed with phylogenetic systematics (Hennig, 1966). Although human paleontology is evolutionary it is not necessarily populational, tending rather towards typology as embodied in "character states" instead. Its adherents tend to believe in the supremacy of the fossil record, or more precisely, in morphology alone, in interpreting hominid evolutionary history. In general its adherents tend to be taxonomic splitters, dismissive of molecular evidence of evolutionary relationships, and concerned with traits or series of traits which are interpreted as primitive or derived (Hennig, 1966). Context, which is of critical concern to paleoanthropologists in the first two paradigms, occupies a less important position in the human paleontology paradigm. These paleoanthropologists tend to be primarily interested in "vertical" questions, such as phylogenetic relationships, and rarely deal with questions of behavior in human evolution. They think of themselves as dealing with the "hard evidence," i.e. skeletal parts (cf. Delson, 1985). Many of the paleoanthropologists who work within this paradigm are members of the Society of Vertebrate Paleontology. Their papers also appear in the *American Journal of Physical Anthropology* and *Journal of Human Evolution*, but they may tend to publish in such journals as *Journal of Vertebrate Paleontology* and *Paleobiology.*

The evolutionary biology paradigm has been ascendant in paleoanthropology since the 1950 Cold Spring Harbor Symposium on "the Evolution of Man." Major early publications were Washburn (1951) and Bartholomew and Birdsell (1953). The cultural perspective is most in evidence today in archaeology, but it probably has had significant impacts on "physical" paleoanthropology with the single species hypothesis (Wolpoff, 1971) and behavioral reconstructions of fossil hominids (e.g. Isaac, 1978; Bar Yosef, 1989). What is termed here the "paleontological" perspective has been injected relatively recently into debates on hominid systematics and one reflection of this influence can be seen in a greater emphasis on splitting in hominid taxonomy, e.g. Tattersall (1986), Groves (1989), Grine (1988), Wood (1991), Rightmire (1996), and Larick and Ciochon (1996). Very few paleoanthropologists fit neatly into one or another of these groupings, and borrowing from other paradigms is common.

THE IMPACT OF PHYLOGENETIC SYSTEMATICS

Naming of species in biology is termed "taxonomy" and the scientific discipline on which taxonomic decisions are based is termed "systematics". Although the basic binomial system of nomenclature used by paleoanthropologists and other biologists goes back to Linnaean typology, the basic theory on which systematic decisions are (or should be) made is population-based neo-Darwinian natural selection. However, the Linnaean system and traditional systematics as used on living species are not well-adapted for expressing evolutionary relationships.

A structured approach to sorting out and expressing phylogenetic relationships was developed by Willi Hennig (1966). It is termed "phylogenetic systematics" or "cladistics" (Harrison, 1993). Its fundamental tenet is that primitive ("plesiomorphic") characters in morphology, i.e. those inherited from ancestral species, are of no use in determining evolutionary relationships among species. Only derived ("apomorphic") characters are to be used in strict Hennigian systematics. The neatness and conciseness of this method compared to the unruliness of the actual hominid fossil record have proved irresistible to many paleoanthropologists who now routinely use the terms of phylogenetic systematics. The key issue in using this method is the initial choice of characters for analysis. If too few are used, if traits are chosen which co-vary within one morphological region, and if characters are variably expressed, then the method breaks down.

Paleoanthropologists who have applied Hennigian principles to the hominid fossil record have promulgated taxonomic splitting. For a field, perhaps more than any other, that was tremendously overburdened with unnecessary fossil taxa (Campbell, 1965), paleoanthropology has not been quick to embrace suggestions for recognizing new taxa. Despite a number of vying interpretations, the taxonomic unity of *Australopithecus afarensis* (see Boaz, 1988), *Homo habilis* (see Tobias, 1991), *Homo erectus* (see Rightmire, 1990), and *Homo sapiens* (see Stringer, 1990) have maintained general acceptance. Use of the generic nomen *Paranthropus* to refer to the robust australopithecines, however, has seemed to gain many followers, e.g. Grine (1988). Some workers recognize the taxa *Homo ergaster* and *Homo rudolfensis* in addition to *Homo habilis* within the pre-*erectus Homo* hypodigm, *Homo heidelbergensis* for European or non-African early *Homo sapiens*, and *Homo neanderthalensis* as a distinct middle to late Pleistocene species in the circum-European region.

An issue of taxonomy which is of some consequence is the choice of nomen to refer to the zoological family to which humans belong. Traditionally this is Hominidae, but phylogenetic systematists, such as Delson (1986), have preferred to use Homininae for this group, reserving the family level taxon for the apes of modern aspect and humans. While this represents an internally consistent cladistic arrangement working from the non-human higher primates inward towards humans, it leaves what to many paleoanthropologists is an unacceptably narrow taxonomic grouping for the morphological and adaptational diversity seen in apes and fossil hominids. Most paleoanthropologists have continued to use the taxon Hominidae for the bipedal members of the Hominoidea (humans and their fossil relatives). The taxa Panidae, with or without Gorillidae, and Pongidae refer respectively to the extant "out-groups" of chimpanzees, gorillas, and orangutans.

SYSTEMATICS: POPULATION VARIABILITY AND TOTAL MORPHOLOGICAL PATTERN

The biggest bugaboo of paleoanthropological systematics is delimiting the variability seen in samples of hominid fossils and interpreting whether this variability is population variability or whether it represents the presence of different taxa. Old intellectual battlefields strewn with slain systematic hypotheses bear witness to the difficulty of this endeavor. There are some guidelines, however.

The first and most important general rule guiding whether different taxa ought to be recognized is that hominid species should show the same degree of morphological difference between them as do other well-recognized species of vertebrates. Applying this rule becomes difficult at times because choice of measurements of morphological distance vary with the investigator, adaptational complexes that differentiate some species do not differentiate others, sexual dimorphism may increase metrical and shape differences within a species, and time averaging over the life-time of a paleospecies may increase variability seen in a fossil sample. A good example of the use of this approach is Eckhardt's (1987) demonstration that the nasal bone configurations of extant great apes show all the patterns of variation that had been postulated by Olson (1985) to differentiate two different taxa within the Hadar australopithecine sample.

A second important rule governing the recognition of fossil hominid taxa is whether the anatomical traits, metric values, and characters chosen to distinguish a taxon are understandable within a functionally interrelated morphological complex. This point is perhaps best expressed by pointing out the difference between "anatomy," which is simply the "cutting up into pieces" of body form, whereas "morphology" is the "study of form" of the body and its parts, as originally defined by Goethe (1796). Wilfrid Le Gros Clark (1964) applied the term "total morphological pattern" to this understanding of a species' particular suite of anatomical characteristics. Tobias (1985) provided a good update on the concept and its application in relation the fossil record of Hominidae.

FACTORING IN MOLECULES

No other part of paleoanthropology represents the clash of the evolutionary biology and paleontological paradigms better than the interaction between primate paleontologists and molecular anthropologists. Paleontologists either outright rejected molecular evidence for the late evolutionary divergence of hominids and apes or considered it merely another character state to be factored in with the rest of the morphology. But molecular evidence cannot be discounted, because it is also measuring what paleontologists wish to understand — the evolutionary divergence and distance between species. Rather than considering molecular data in the same framework as anatomical traits, it is perhaps better viewed as a complementary method of phylogenetic analysis. With unambiguous molecular measures of species relatedness paleontologists now have an additional way to sort out homologous and non-homologous traits in systematics.

The most well-known recent case of molecular-paleontological paradigm clash has been the Mitochondrial Eve or "Out of Africa" debate relating to the evolutionary origins and migration of anatomically modern *Homo sapiens*. Some specifics of this debate will be discussed below. At this point the theoretical predispositions of the molecular (evolutionary) and paleontological sides will be noted.

Paleoanthropologists within the paleontological paradigm tend to regard character traits as metaphors for the entire organism. We might borrow the term "anatomical metaphor" from the literary world for this approach, as when we refer to "all hands on deck" or so many "head of cattle." We obviously are not referring to the named anatomical parts but to the whole organism. In the same way paleontological-paradigm paleoanthropologists may draw diagrams of one tooth form evolving into another when they really mean that the organism that possessed that tooth form lived in a population that gave rise to other individuals with the same or modified tooth form in later populations. The fact that Zhoukoudian *Homo erectus* had shovel-shaped incisors does not necessarily mean that this population gave rise as a unit to modern Chinese, who also tend to have shovel-shaped incisors.

Molecular anthropologists also suffer from the metaphor problem. They tend to think of a molecule as synonymous with the organism, and this is perhaps due in part to the unfortunate fact that organismal biology is on a rapid decline in biology departments worldwide. In fact, molecules exist within an organismal framework, and like anatomical traits they can have their own evolutionary lineages distinct from the organisms of which they form a part (Ayala, 1995). Thus, there is an important distinction between gene lineages and organismal lineages, a point to which we will return.

The rapidly advancing developments in understanding the molecular basis of morphology, particularly the role of homeotic genes (see Weiss, this volume), promise a much more fundamental understanding of the relationships between the character traits that paleontologists have traditionally used and their true biological meaning.

STRUCTURE, FUNCTION, BIOLOGY, AND BEHAVIOR

The "horizontal" questions with which paleoanthropologists are concerned, i.e. those that relate to the past life of a species during the time that it was alive, are addressed in three major ways through research and analysis. The first is by direct study and interpretation of the fossils themselves. Studies of the form and dimensions of hominid postcrania (Trinkaus, 1983), dental microwear studies (Grine and Kay, 1988), comparative studies of vocal tract anatomy (Laitman and Heimbuch, 1982), growth studies based on enamel microstructure (Smith, 1991), and isotope analyses of bone and teeth for dietary reconstruction (Sillen et al., 1989) are all examples of this hominid fossil-based type of analysis. This is the domain of the "physical anthropologist," i.e. a paleoanthropologist who studies the actual remains of hominids themselves. The second method is by study of the contexts in which hominid fossils are found. The third method is by interpretation of cultural remains recovered in the archaeological record. This archaeological component of paleoanthropology is most important in the latter phases of human evolution when remains of material culture become relatively abundant, and it is largely outside the scope of this review.

IN PURSUIT OF CONTEXT: TIME, PLACE, AND NATURAL HISTORY IN HUMAN ORIGINS RESEARCH

The fundamental reason that the approach of simple seriation of hominid fossils into phylogenetic lineages does not result in profound understanding of human evolution is that the evolutionary process has been a complicated system of biological interactions over millions of years. That evolution is indeed such a system with complicated networks of interspecies and environmental interactions was recognized by Ernst Haeckel, who coined the term "ecology" (1868). "Paleoecology" is the attempt to interpret this dynamic view of evolutionary change into the past. Bartholomew and Birdsell (1953) published the first important paper in hominid paleoecology. The current active topics of research in hominid taphonomy (e.g. Behrensmeyer and Hill, 1980; Shipman and Harris, 1988; Klein, 1994), evolutionary change in the hominid career resulting from significant climatic change (e.g. Brain, 1981; Boaz and Burckle, 1985; Vrba, et al., 1995; Potts, 1996), and the significance of early hominid scavenging compared to gathering and hunting (Blumenshine, 1987) fall within this arena of paleoanthropological endeavor.

This approach has sometimes led paleoanthropologists apparently far afield. Anthropology doctoral dissertations on the evolution of Miocene fossil horses (Raymond Bernor, UCLA, 1978) and on Plio-Pleistocene fossil hippopotamids (Paris Pavlakis, New York University, 1982) are two examples. These and other similar studies on fossil groups associated with anthropologically relevant sites provide important contextual information of the evolution of apes and hominids in these periods of time.

The increasing importance of context in human origins research, and the fact that much of this multidisciplinary effort is carried out by scientists without anthropological training, led Boaz (1992) to use the Haekelian term "anthropogeny" to refer to this new field. Such workers as geophysicists Garniss Curtis, Carl Swisher, and Paul Renne of the Institute of Human Origins and Berkeley Geochronology Center, Frank Brown and Thure Cerling of the University of Utah, and Stephen Weiner of the Weizmann Institute of Science, paleobotanists Raymonde Bonnefille of the Centre National des Recherches Scientifiques in Marseilles and Gregory Rettallack at the University of Oregon, not to mention many molecular biologists and geneticists, have focused on human origins as a major theoretical orientation. They have drawn significant research funding from traditional anthropological sources, their discoveries have broken new theoretical ground (and frequently made headlines), and their perspectives have been informed by close collaboration with paleoanthropologists and a thorough knowledge of the paleoanthropological literature. Yet the method and theory that these scientists employ are not taught in any anthropology graduate program in the United States, and it is not possible for a graduate student to obtain a degree in any of these disciplines within a traditional Anthropology Ph.D. Perhaps a new term for the field is needed, or perhaps it is time for paleoanthropologists to redesign their university curricula to keep up with what is undoubtedly one of the most profound changes in research directed at knowledge of human origins.

MAJOR RECENT DISCOVERIES IN PLIO-PLEISTOCENE PALEOANTHROPOLOGY

Much ink is spilled on the importance of paradigms and the frameworks in which hominid evolution is viewed. Recent interest in the narrative nature of hominid evolutionary scenarios (Landau, 1991) and an orientation that takes a female evolutionary perspective into account (e.g. Lancaster, 1993) are examples. There is more than a little justification for these points, but it has been my contention (Boaz, 1982) that progress in understanding the course of hominid evolution historically is traceable not to paradigm shifts *per se* or to "ways of looking at" the data, but to the data themselves, to new discoveries. If one judges the progress in paleoanthropology on the basis of new discoveries, then the field is doing well. Figure 1 shows the location of hominid fossil sites discussed in the following text.

CALIBRATION OF THE HOMINID FOSSIL RECORD

Knowing the age of a hominid fossil is now basic to an understanding of its evolutionary significance. The lack of reliable contextual data on virtually all of the discoveries of fossil hominids before the latter half of this century is a testimonial that this realization is a relatively recent one for paleoanthropologists. Also, some cladists have lately maintained that geological age of a fossil is irrelevant in determining its phylogenetic position because this information should be gleaned entirely from the morphology of the fossil and the fossils to which it is compared. This comfortingly circular logic is rarely heard nowadays, with cladists focusing instead on using the morphology alone for the construction of cladograms. When a time component is added and actual ancestor-descendent relationships are postulated, a phylogeny results. It is easy to see that if a fossil that has primitive morphology lived at a

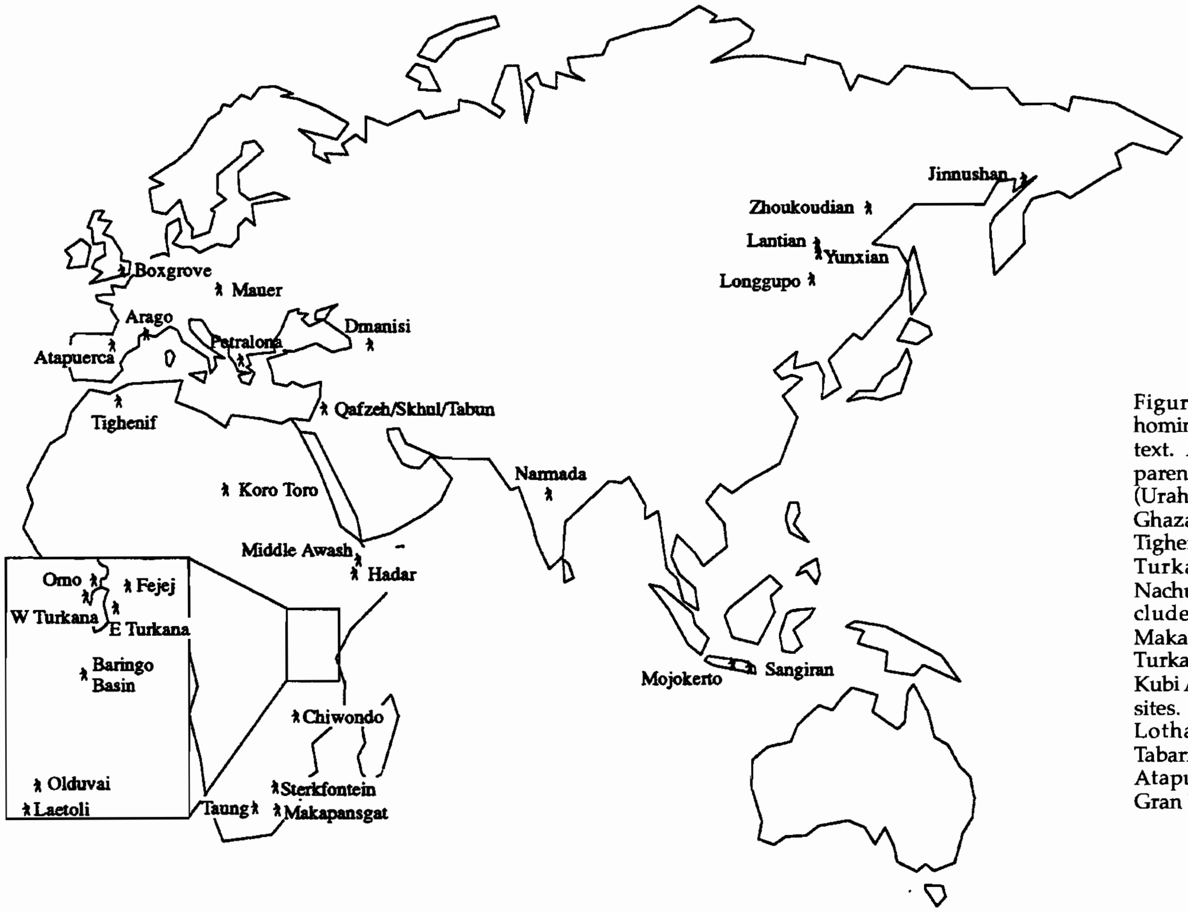

Figure 1. Important fossil hominid sites discussed in the text. Alternate site names (in parentheses) are: Chiwondo (Uraha), Koro Toro (Bahr El-Ghazal), Mauer (Heidelberg), Tighenif (Ternifine), and West Turkana (Nariokotome/Nachukui). Middle Awash includes Aramis, Belohdelie, Maka, and Bodo sites. East Turkana includes Koobi Fora, Kubi Algi, Ileret, and Allia Bay sites. Baringo Basin includes Lothagam, Chemeron, Tabarin, and Tugin Hills sites. Atapuerca includes SH and Gran Dolina sites.

later geological time period than one that has more derived morphology, then the former cannot be a member of the population that was ancestral to the species that contains the latter specimen. Of course, if phylogenetic systematics (or any systematic methodology) were perfect and we had large numbers of complete skeletons to do our analyses then perhaps morphology alone would be less prone to error. Under real circumstances, however, knowing the geological time period in which a fossil lived is a very important piece of data.

As more and more interest has been focused on the environmental and climatic contexts of fossil hominids, geological provenance has become of ever-increasing significance as well. Comparisons of distant events that might be coupled with events in hominid evolution must be accurately known.

Some of the most heated debates in paleoanthropology in the last twenty years have involved the geological ages of fossil hominid sites. Debates that were resolved were the age of the KBS Tuff at Koobi Fora, Kenya (ca.1.8 ma; Brown, et al. 1978, 1985; for popular accounts see Leakey and Lewin, 1977; Johanson and Edey, 1981, and Boaz, 1993), and the age of the KMB level at Hadar (Brown, 1982, 1994, but see Walter and Aronson, 1993). The geological age of the Olduvai hominids, the first that were dated using the then-new potassium-argon technique (Curtis and Evernden, 1962), was one of Louis Leakey's most effective arguments for the significance of Olduvai Gorge (e.g. Leakey, 1961). The "oldest" is still a superlative that attracts a lot of attention in the media as well as in scientific circles, but there are needs for accurate dating at all levels of the hominid fossil record. Two of the most profound dating discoveries in recent years have been the establishment of the antiquity of early *Homo* levels in Asia at 1.8 — 1.9 ma, and dating of *Homo sapiens sapiens* earlier than Neandertal levels in Israel at some 100 ka. While neither of these datum points are the earliest records for their respective hominid taxa, they do contribute important information in putting together the global pattern of hominid evolution.

THE YARDSTICK OF OMO - TURKANA BASIN GEOCHRONOLOGY

Africa, at least insofar as human evolution is concerned, seems to uphold Herodotus's oft-quoted statement that "ex Africa semper aliquid novi" [out of Africa there is always something new]. Africa is the largest land mass spanning the ancestral tropical environments of hominids, it is subject to habitat partitioning by past climatic and geological changes, because of its biotic productivity the tropics may tend to be generators of new species, and Africa today still retains more human genetic variation than the rest of the world combined. For whatever combination of reasons, Africa has held on to its claim, first staked out by Louis Leakey, as the "birthplace of man." The advent of absolute dating methods was a critical part of establishing Africa's primacy in the appearance of hominids in the fossil record.

As is generally known the Plio-Pleistocene sediments in the East African Rift System preserve many volcanic, potassium-rich rocks. The formation dates of these rocks are datable by the potassium-argon technique and its newer version, argon 40-39 dating (Curtis, 1993). At no other place has this dating methodology been taken to a higher level of refinement than at Omo and the Turkana Basin, where Frank Brown and colleagues have systematically built up a sequence extending from over 4 ma to less than 1 ma (Brown, 1994). The geochronological sequence of Brown was based on the detailed stratigraphic work of de Heinzelin (1983) at Omo, and it is bolstered by high resolution paleomagnetic reversal chronology, fission track dates, detailed vertebrate and invertebrate biostratigraphy, and correlation to deep sea sediments. Brown developed a technique of chemically "finger-printing" the volcanic tuffs at Omo and then correlating them across large areas in the Turkana Basin. The temporal control that this framework provides has been invaluable in the hominid-rich series of sites in the Turkana Basin. Delta Willis (1989) has provided the best popular account of Brown's work. Figure 2 is an overview of Turkana Basin geochronology with tuff correlations to other regions and ranges of hominid taxa indicated.

THE AGE OF THE EARLIEST STONE TOOLS

The question of when hominids first began using tools has been of interest to paleoanthropologists for quite some time because of the importance that tool-use has assumed in many scenarios of hominid evolution, including that of Darwin's (1878). The fact that stone preserves so well has meant that the operationalization of this question has come down to the use of stone tools.

J.W.K. Harris (1986) has been perhaps the most active archaeologist investigating the period of the earliest stone tool cultures, which occur in Africa. He and his teams have excavated sites in the Turkana Basin, Hadar, and the Semliki Valley, Zaire, that are now dated among the oldest stone tool sites known. Sites at Omo excavated by Chavaillon and Merrick

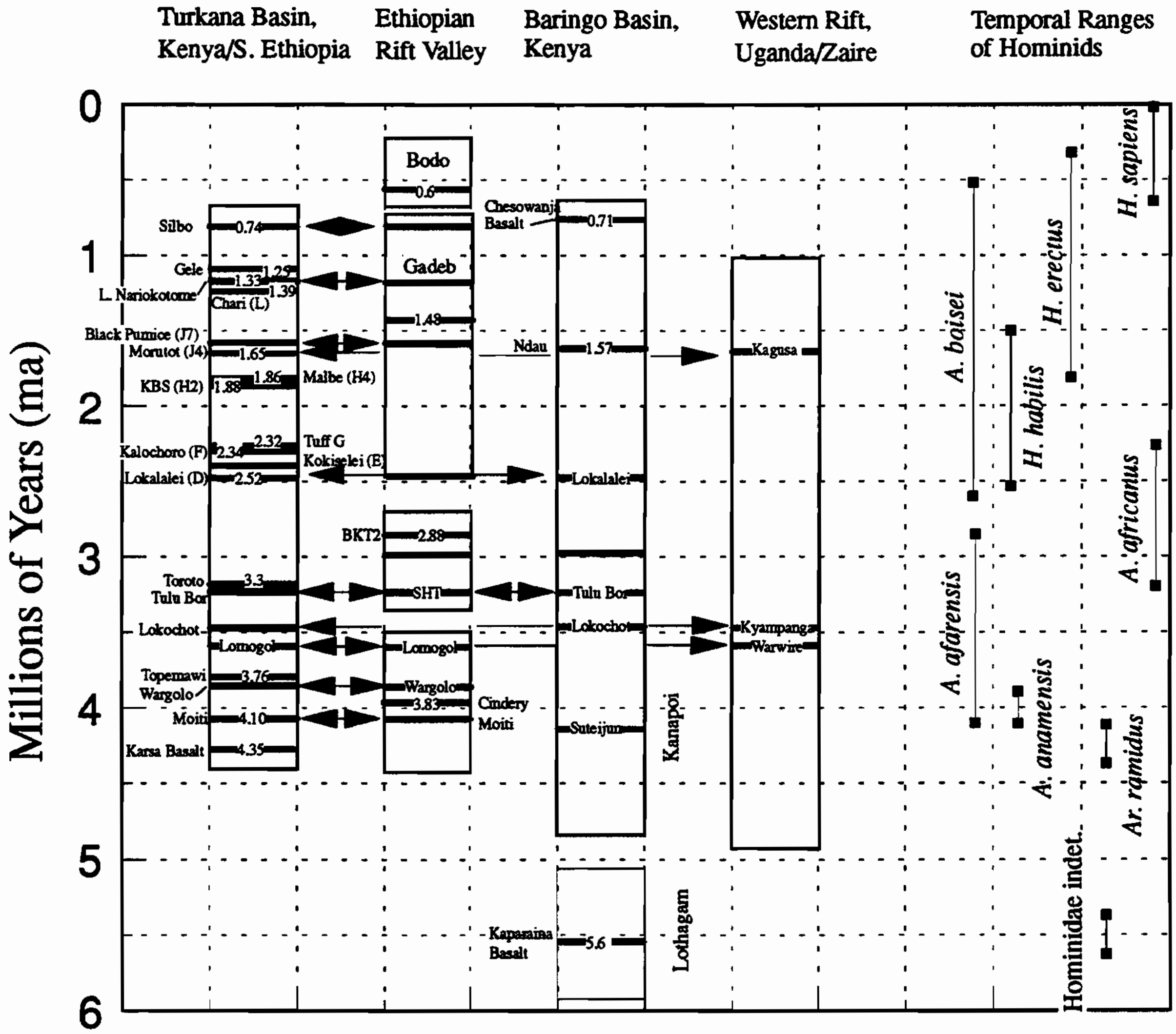

Figure 2. Geochronology of the Omo-Turkana Basin sequence, Ethiopia/ Kenya, with tuff correlations to the Ethiopian Rift, Baringo Basin, and Western Rift indicated. Ranges of hominid taxa are indicated (dates and tuff correlations from Brown ,1994).

(Merrick, 1976), in Malawi, and in western Uganda are also among the earliest known occurrences. These sites date to around 2.5 ma and younger. These stone tools occur mostly in fine-grained sediments and would have to be classified as "manuports" (brought in to the deposit by human agency) even if they did not show clear human breakage patterns. They are very simple tools, having been in many cases made from quartz. They thus differ in this respect from later stone tools at Olduvai Bed I, for example, that are made primarily from basalt and other unveined crystalline rocks. The earliest appearance of stone tools corresponds to the earliest recognition of the genus *Homo* in the fossil record, and general opinion holds that these two events may be correlated. Kibunjia (1994) has termed these earliest tools the "Omo Industrial Complex."

The appearance of stone tools in the record is an important datum, but some researchers such as Lovejoy (1981) have mistakenly taken it as the datum for general tool use in hominid evolution. Brain (1985) has now convincingly shown that bone tools are present in the cave of Swartkrans, and although these tools are only slightly earlier than the earliest stone tools in eastern Africa they demonstrate that australopithecines could also make and use tools.

AGE OF ASIAN *HOMO ERECTUS* AND IMPLICATIONS FOR EXPANSION OF HOMINIDS OUT OF AFRICA

Swisher et al. (1994) reported that they dated pumices recovered from two early hominid sites in Java, Indonesia at 1.81 ± 0.04 ma (the site of Mojokerto) and 1.66 ± 0.04 ma (sites at Sangiran) using the recently developed argon-40/argon-39 laser-fusion technique. These results with impressively low ranges of error were in stark contrast to Curtis' previous dating of a pumice from near Mojokerto to 1.9 ± 0.5 ma using conventional potassium-argon dating (Jacob and Curtis, 1971). Swisher, et al. first compared the geochemistry of samples of the mineral hornblende from sediment still inside the cranium of the juvenile hominid skull from Mojokerto (named *Homo modjokertensis* by von Koenigswald, 1936) with sediment from the excavation that yielded the skull in 1936. For all 11 oxides tested there was close agreement. Thus by both field confirmation of the site of excavation and the geochemical results they established the geological provenance of the Mojokerto specimen. There were no hornblende samples large enough for dating inside the cranium so Swisher, et al. took samples from the excavation sediment. These analyses yielded 4 independent results with the mean age of 1.8 ma cited above. To further confirm the date they ran paleomagnetic analyses and confirmed that the sediments at Mojokerto were "normal" in polarity. Earlier geological investigators had also found normal polarity but had interpreted this to be the "Jaramillo Event", dating to about 1 ma. Swisher et al. instead interpreted the normal polarity to be indicative of the "Olduvai Event" dating to ca. 1.9 ma, and thus in agreement with the argon 40-39 date. Results using similar techniques from Sangiran, from which several *Homo erectus* fossils were found in the excavation of an irrigation ditch in 1974, yielded the date of 1.6 ma.

There will inevitably be debate concerning the re-dating of the classic Javan *Homo erectus* sites, but there is much to support the position of Swisher, et al. (1994). Pope (1983, 1988) has been the most active advocate for a late date for the appearance of hominids in Asia, suggesting that there are no sites with unequivocal dates earlier than 1 ma. But most of Pope's argument on the late dates for Javan *Homo erectus* relies on the uncertainty that has surrounded the provenance and geochronology of the hominid fossils. The new results by Swisher, et al. (1994) significantly increase both the probability that Javan fossil bearing sediments date to 1.8 ma at Mojokerto and 1.6 ma at Sangiran, and that hominids derive from those fossiliferous levels.

An "early" date for the hominid-bearing deposits of Java was also proposed by Ninkovich and Burckle (1978) and by Ninkovich et al. (1982) who correlated deep sea sediments with marine/non-marine stratigraphic sections exposed in Java. These authors utilized diatom fossil occurrences, correlations of tektite deposits on land with microtektite levels in the deep sea, and deep sea paleomagnetic reversal stratigraphy to infer an age for the base of the hominid-bearing Putjangan Beds of between "about 1.9 ma BP and 2.1 ma BP" (Ninkovich et al., 1982:220). These authors constructed a paleogeographic map for the Sunda Shelf region surrounding Java. Based on the record of oxygen isotope changes they postulated that Java would have been separated from mainland Asia until 2.4 — 3.0 ma. As late Pliocene glaciation in the Northern Hemisphere locked up seawater and lowered sea level, fauna and hominids could have dispersed from Asia to Java via Malaysia and Sumatra.

The importance of this conclusion is that hominids must have been present in mainland Asia 1.8 million years ago and possibly earlier. The implication is that pre-*erectus Homo* may also be present in Java and indeed in other parts of Eurasia (cf. Tobias and von Koenigswald, 1964; Larick and Ciochon, 1996). Major excursions of the oxygen isotope curve at ca. 2.8 ma and ca. 1.7 ma (Figure 3) with attendant global cooling and generally more arid terrestrial climates (deMenocal, 1995) may be causally linked to these dispersal events.

Two other early datum points have been reported for Eurasian early *Homo* and these also represent important advances in our knowledge. The first of these is the cave site of Longgupo, central China. The age of this site is based on biostratigraphic assessments of an abundant fossil fauna, paleomagnetic attribution to the Olduvai Event (1.96 — 1.78 ma), and a capping electron spin resonance date of 1.02 ± 0.1 ma (Huang et al., 1995). A hominid mandible and fragments of dentition have been attributed to pre-*erectus Homo* or to a *Homo erectus* population more primitive than Zhoukoudian. The second site, Dmanisi in the Georgian Republic, is west of the Ural Mountains and is thus west of the boundary between Europe and Asia (Figure 1). It has yielded a fauna that is "late Villafranchian" in character and which rests on a basalt dated to 1.8 ma (Gabunia and Vekua, 1995). The normal paleomagnetic polarity has also been interpreted as within the Olduvai subchron. The depositional context of the Dmanisi hominid specimen, a mandible with full dentition, is not primary, however. A study of the mandible by Bräuer and Schultz (1996) supported an attribution to *Homo erectus* but also noted "progressive" features in the symphyseal and dental morphology that could indicate a somewhat later date for Dmanisi. Taken together, the Mojokerto, Longgupo, and Dmanisi discoveries nevertheless lend support to the basal Pleistocene presence of *Homo* in Eurasia.

ECOLOGICAL CHANGE AND HOMINID EVOLUTION

Coupled with increasingly accurate geochronological control, paleoclimatic data from deep sea (a more continuous record) and terrestrial (a more direct but more discontinuous record) sources have provided our first good overall view of the paleoclimatic conditions attendant to Plio-Pleistocene hominid evolution. The use of isotopes of oxygen (^{18}O, which is preferentially locked up in glacial ice during cold periods) and carbon (^{13}C, which is involved in the C-4 metabolic pathway characteristic of grasses) in assessing past environmental change has been of paramount importance in these studies. Figure 3 depicts recent deep sea and soil carbonate isotope curves for the Plio-Pleistocene (Boaz and Burckle, 1985; deMenocal, 1995). They show two clear trends during the past five million years: an overall mean trend towards globally cooler climates as one approaches the present, and a trend of increasingly severe climatic oscillations around this mean as one approaches the present. DeMenocal (1995) dated the onset of a 41,000-year periodicity to about 2.8 ma and the onset of a 100,000-year periodicity to about 1.0 ma. Despite this evidence and other attempts , e.g. Vrba et al. (1995) to find cataclysmic climatic events and tie them to phylogenetic change in hominid evolution, correspondences have yet to be agreed upon. In very general terms, it does appear that hominids began to occupy a world less wooded than that of their Miocene forebears, and that the genus *Homo*, appearing at ca. 2.5 ma, became adapted both to progressively colder mean temperatures, as well as to periodically more extreme cold and warm environments, as the Pleistocene progressed. Potts (1996) has recently suggested the term

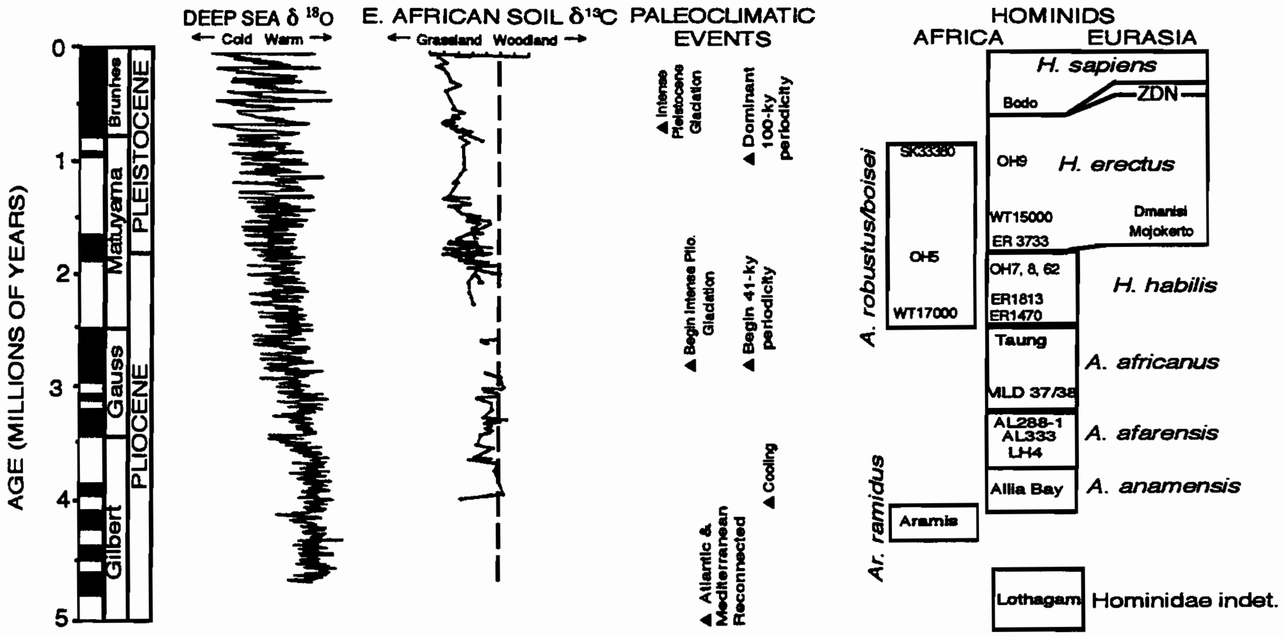

Figure 3. A paleoclimatic framework for Plio-Pleistocene Hominidae (revised from Boaz and Burckle, 1985, and with data from deMenocal, 1995).

"variability selection" to refer to the evolution of hominid bio-behavioral adaptations that would necessarily have had to accompany these climatic shifts. There are many data points in the terrestrial fossil hominid record that blur these general trends and underscore the wide range of adaptability of especially later hominids in this time range. Regardless of our theoretical predispositions, the overall climatic record seems to indicate an overall gradual, if marked, pattern of change throughout the Pliocene and Pleistocene.

NEW DATES FOR ARCHAIC HOMO SAPIENS AND *HOMO SAPIENS SAPIENS* SITES

The period of geological time after about 1 ma and before 50,000 y has been a sort of "No Hominids' Land" insofar as accurate geochronology is concerned. This is because this time period is too young for accurate potassium-argon dating and too old for carbon-14 or radiocarbon dating. Some progress has been made in extending the effective time frames for both methods using increasingly accurate methods of counting isotopes (cf. Curtis, 1993).

Clark et al. (1994) report a ^{40}Ar-^{39}Ar laser-fusion date of 0.64 ± 0.03 ma on feldspars from a tuff near Bodo, northern Ethiopia. Despite the presence of a fault and an unknown stratigraphic distance intervening between the dated horizon and the locality of the archaic *Homo sapiens* skull from Bodo, these authors interpret the age of the hominid as "approximately 0.6 million years old" on the basis of biostratigraphic similarity between the dated level and the level of the hominid. If correct, this date could indicate that morphologically similar and poorly dated archaic *Homo sapiens* from Petralona (Greece) and Yunxian (China) may be of similar antiquity.

Real advances have also been made using thermoluminescence (TL) and electron spin resonance (ESR). Aitken (1985) provides an introduction to TL dating, and a general treatment of ESR dating with applications to *Homo sapiens* evolution can be found in Grün and Stringer (1991). One of the most important areas that has been dated using these techniques is the late Pleistocene fossil hominid record in the Near East, particularly Israel, which has occupied a central place in the formulation of scenarios for the evolution of modern *Homo sapiens* for quite some time, e.g. McCown and Keith (1939).

Two major conclusions stand out in recent geochronological work in Israel. The first is that anatomically modern *Homo* sapiens was present here at the site of Qafzeh between 92,000 to >100,000 y (Valladas et al., 1988; Schwarcz et al., 1988; Grün and Stringer, 1991), at an antiquity equal to or nearly equal to that in African sites such as Border Cave, Klasies River Mouth, and Omo Kibish (Grün and Stringer, 1991). By contrast, the earliest record of anatomically modern *Homo sapiens* in Europe date to about 45,000 y (Porat and Schwarcz, 1994). Secondly, new dating of the classic sites of Skhul (anatomically modern *H. sapiens),* Tabun *(H. s. neanderthalensis)* and Kebara *(H. s. neanderthalensis)* show that the Levantine Neandertals appeared not only *before* anatomically modern *Homo sapiens* but *in between* levels containing anatomically modern *Homo sapiens.* This redating forces re-framing of hypotheses of Late Pleistocene hominid evolution (Bar Yosef, 1989, and see below). Tabun also has early Neandertals, coeval with Qafzeh (Stringer, 199).

EXTENDING THE PLIO-PLEISTOCENE FOSSIL SAMPLE

A standard byline of media reports and some scientific journal papers describing the newest hominid fossil discovery is that "it overturns all previous conceptions" or "the textbooks will now have to be re-written." These statements are usually hyperbole. But significant progress has been made in recent years in extending the sample size, the geographical spread and temporal spread of the known hominid fossil record. The major recent discoveries are reviewed by geographic area below.

AFRICA

The earliest fossil record of hominids occur on the African continent. Hill (1994) provides a good review of the sites and the scanty fossil remains of these earliest harbingers of our lineage. Perhaps the only serious suggestions that the earliest hominids are to be found anywhere but the African continent is that by de Bonis and Koufos (1992) who argue that the Greek late Miocene *Ouranopithecus macedoniensis* represents a phyletic hominid. There are some aspects of the facial morphology that seem to connect these apes with African hominoids but there are no clear features of the dentition that link this species with the later African early hominids. The zoogeographical pattern of such a relationship would also be very difficult to understand in the context of what is known of early hominid and African ape distribution (see Boaz, 1994).

The earliest hominids known occur in the Baringo Basin of Kenya and they date from around the Mio-Pliocene boundary, at an estimated age of 5.6 — 5.8 ma for the Lothagam mandible (Hill et al., 1992) to 4.5 ma for the Tabarin mandible and Chemeron humerus.

Other early records of hominids dating to between 4.5 and 3.8 ma are also all quite fragmentary. These records include the Middle Awash and Fejej sites in Ethiopia, and in the Turkana Basin of Kenya, the lowest levels at Koobi Fora and the site of Kanapoi. A number of these remains are attributed to *Australopithecus afarensis* or compared to it (Boaz, 1988; Hill,1994; White et al., 1994a; Kappelman, et al. 1996) but their fragmentary nature makes these attributions less than firm. White et al. (1994b, 1995) coined the taxon *Ardipithecus ramidus* on the basis of fragmentary chimp-like dental and basicranial remains from the Middle Awash site of Aramis, dating to ca. 4.4 ma. M.G. Leakey et al. (1995) named *Australopithecus anamensis* on the basis of specimens from sediments 3.9 to 4.2 million years old at Kanapoi and Allia Bay, Kenya (Coffing et al. 1994). The Fejej remains (Fleagle et al., 1991) have recently been re-dated to 4.0 — 4.2 ma (Kappelman et al., 1996), and these latter authors have interpreted the near-contemporaneity of fossils attributed to *A. afarensis*, *Ar. ramidus*, and *A. anamensis* to indicate phylogenetic diversity in early Pliocene hominids.

A dramatic demonstration of an enlarged geographical range of Pliocene *Australopithecus* in Africa came with the publication by Brunet et al. (1995) of a new discovery in central Chad (Figure 1). KT12/H1 (Koro Toro site 12 at Bahr El-Ghazal) is a mandible lacking both rami but preserving an intact symphysis and RI$_2$-P$_4$ and LC-P$_4$. The specimen shows a high symphysis and a large canine as well as molariform, three-rooted premolars with reportedly thin enamel! It was assigned to *A.* aff. *A. afarensis* and dated biostratigraphically to between 3.0 and 3.4 ma by comparison with Omo and Hadar. Perhaps most significant is its location in the Lake Chad Basin, some 2500 km to the west of the East African Rift System. Unlike early Pliocene/late Miocene faunas in northern Africa, such as Sahabi, which are biotically quite distinct from eastern Africa, the Bahr El-Ghazal fauna so far as is known is identical in species composition to penecontemporaneous eastern African sites.

Southern Africa, which is rich in australopithecines, largely lacks fossiliferous deposits in the early Pliocene. The one site of Langebaanweg near the Cape of Good Hope coast, which is otherwise a rich repository of early Pliocene fauna dating to approximately 4 to 5 ma, has given up no hominoids and almost no primates (Klein, 1994).

Important field research in this general time is actively underway by several expeditions. In the Eastern Rift Valley, teams led by Tim D. White in the Middle Awash are working in areas dating to between 3.4 and 4.4 ma, and several new hominid specimens have been recovered (White et al., 1994a, b). The fauna recovered from the early site of Aramis, which includes *Ar. ramidus*, is remarkable in its indications of forest-adapted species. Andrew Hill's Baringo Palaeontological Research Project is continuing to work at the Tugen Hills site. Meave Leakey directs a team that is continuing work at the Lothagam site. The Wembere-Manonga Palaeontological Expedition led by Terry Harrison is investigating fossiliferous sediments in northern Tanzania that date to 4 to 6 ma that have so far not yielded any hominid remains but are rich in other mammal fossils (Harrison et al., 1993).

In the Western Rift Valley teams led by Noel Boaz (Semliki Research Expedition, Zaire, and Western Rift Research Expedition, Uganda), and by Martin Pickford and Brigitte Senut (Uganda Paleontology Expedition), have investigated fossiliferous sediments in the early Pliocene/late Miocene, as well as later time periods (Boaz, 1994). Paleonvironemnts vary from forested to wooded savanna at different time periods in the Western Rift. In terms of fossil hominoid fossils only a very fragmentary canine tooth of a putative "gorilline" was reported by Cecchi and Pickford (1989) from Nkondo, western Uganda, dating to ca. 3.5 ma, and a crushed cranium of *Homo* sp. was reported by Senut et al. (1987) from Nyabusosi, Uganda, dating to ca. 1.5 ma based on its reported stratigraphic proximity to the Kagusa Tuff (Figure 2).

In the early Pliocene, paleontological research is actively continuing at the site of Hadar in northern Ethiopia. Kimbel et al. (1994) report the discovery of several new fossil hominids, including a large and presumably male skull (AL444-2). This specimen derives from the top of the Hadar Formation sequence, dating to ca. 3.0 ma. A more lightly constructed face (AL417-1d), presumably from a female, has also been recovered from somewhat lower in the sequence (ca. 3.25 ma). These remains provide a better idea of the variation within the Hadar sample of *A. afarensis*, although interpretations of this variability vary (see below). Other recently discovered remains include an ulna and a humerus.

In the late Pliocene one of the most significant recent hominid discoveries in Africa comes from Malawi. Friedemann Schrenk and Timothy Bromage direct the Hominid Corridor Research Project which has discovered vertebrate fossils at levels ranging in age from 1.5 ma to 3.9 ma, as dated by fauna. A hominid mandible estimated to be some 2.3 ma old was compared to specimens from East Lake Turkana (ER1802) and termed by them *Homo rudolfensis* (Schrenk et al., 1995)).

Two partial skeletons were recovered in recent years both dating to ca. 1.8 — 1.9 ma. Olduvai Hominid 62 (Johanson et al., 1987) was found in Bed I and consists of a highly fragmented skeleton with teeth of an old, but very small individual, attributed to *Homo habilis*. A discovery at East Lake Turkana (KNM-ER 3735) that included hominid cranial and postcranial fragments but no teeth, attributed to *Homo habilis*, was bracketed between sedimentary deposits dated to 1.88 and 1.91 ma (Leakey et al., 1989). These discoveries have played important roles in debates relating to sexual dimorphism, locomotor, functional, and taxonomic diversity in early *Homo*.

In South Africa paleoanthropological work has continued at the sites of Taung and Makapansgat by Jeff McKee, Swartkrans (Brain and Sillen, 1988), and at Sterkfontein (Tobias, 1989). Differences of opinion concerning the ages of the Taung and the paleoenvironmental contexts of the South African cave sites have relevance to the debates on the phylogenetic histories and paleoecological adaptations of the australopithecines. New postcranial remains from Sterkfontein (Clark and Tobias, 1995; Shreeve, 1996) indicate ape-like limb proportions for *A. africanus* and a divergent hallux. Paleobotanical data from Sterkfontein also now show the presence of lianes, climbing vines characteristic of African forest environments, indicating that trees were probably a significant part of the Sterkfontein habitat mosaic. New work at the sites of Gladysvale and Drimolen have produced hominid fossils that are still under study by Lee Berger and colleagues. A new taphonomic study of the Taung skull by Berger and Clarke (1995) suggested that some of the damage to the surface bone was peck marks by a large bird, and that the skull may actually have been transported to its burial site by an eagle!

In the Pleistocene the most complete early hominid skeleton yet recovered, the Nariokotome *Homo erectus* (KNM-WT 15000) from West Turkana, Kenya, was published in monographic form by Walker and Leakey (1993). Nariokotome dates to ca. 1.7 ma. Because the skeleton is so complete it has yielded interesting insights into *Homo erectus* paleobiology, growth (see Bogin, this volume), and body proportions (Ruff, 1993). Body form was long and linear, and proportions were similar to living African populations adapted to hot climates.

EURASIA

Several discoveries in recent years have extended both the time and geographical extent of the Plio-Pleistocene Hominidae in Eurasia, although some of the discoveries have yet to be fully evaluated. Mention has already been made of the early Dmanisi mandible from Georgia and the Longgupo dental remains from China.

A nearly complete skull of *Homo erectus*, informally named Skull IX, was recovered in 1991 at Sangiran, Java, Indonesia (Tyler et al., 1994). As already noted, Sangiran dates to ca. 1.6 ma.

A significant new site of discovery of Pleistocene hominids is Atapuerca, north central Spain (Figure 1). There are two localities at Atapuerca, both of which are karstic in-fillings. The stratigraphically higher of the two localities, Sima de los Huesos (SH), is about 400 ky old, based on fauna. It has yielded some 1300 human fossil remains, attributable to early Neandertals (Arsuaga et al., 1993; Stringer, 1995). A second, older site at Atapuerca, Gran Dolina, is dated near the Matuyama-Brunhes paleomagnetic boundary at some 780 ky (Parés and Pérez-Gonzalez, 1995). It is thus comparable in age to Tighenif (ex-Ternifine), Algeria, and Lantian, China, sites which have yielded remains of archaic *Homo sapiens* and *Homo erectus*, respectively (Figure 1). Carbonell et al. (1995) report the discovery of more than 30 hominids from Gran Dolina and attribute them to "a primitive form of *H. heidelbergensis*," based particularly on frontal bone morphology which differs from the *H. erectus* condition. Gran Dolina seems to support the thesis that that *H. erectus* in Asia was contemporaneous with archaic *H. sapiens* (or a pre-sapiens species such as *H. heidelbergensis*) in Africa and Europe.

Sussex, U.K., whose last widely known contribution to paleoanthropology was the fraudulent Piltdown fossils, has now yielded a real hominid partial tibia from the site of Boxgrove, dating to some 500,000 y on the basis of faunal zonation (Roberts et al., 1994). This is by far the oldest hominid record in Britain and equals the Heidelberg mandible in age. Stringer (1996) ascribes the specimen to *Homo* cf. *heidelbergensis* and notes its large size. Others would assign it to archaic *Homo sapiens*.

In the Narmada Valley of India, a new discovery of a skull that resembles archaic *Homo sapiens* was reported by Sonakia (1985), who compared it to *Homo erectus*. The dating of this specimen is not clear but on faunal and archaeological grounds, it is probably early Late Pleistocene or late Middle Pleistocene, in the range of 100,000 — 150,000 y. It is important as the first clear indication of fossil hominids in India. Kennedy et al. (1991) restudied the specimen and assigned it to archaic *Homo sapiens*.

In China, a discovery made ten years ago at Jinniushan of an archaic *Homo sapiens* skull was dated by ESR and uranium-series dating to the unexpectedly early date of approximately 200,000 y (Tiemei et al., 1994). The authors suggest that its early age, almost as old as some Chinese *Homo erectus* finds, raises the possibility of the coexistence of the two species in China.

ONGOING DEBATES AND DISCUSSIONS

Paleoanthropology is known for the contentious nature of the field. Unfortunately, many of these fiery debates are characterized by more heat than light. The debates discussed below are some of the most active and ongoing in the field of Plio-Pleistocene paleoanthropology.

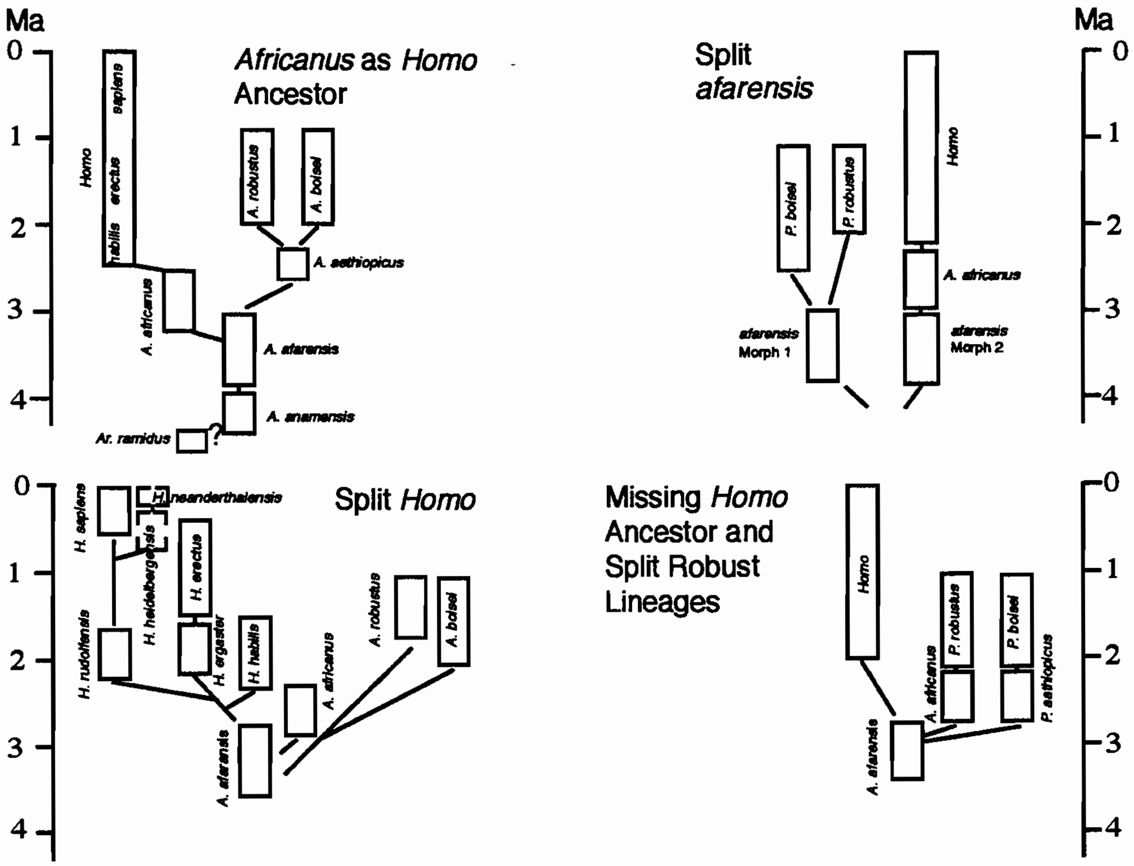

Figure 4. Some representative hominid phylogenies as discussed in the text.

THE SYSTEMATICS AND PHYLOGENY OF EARLY AUSTRALOPITHECINES

Undoubtedly the largest recent volume of new work on the systematics and phylogeny of early hominids has been prompted by the discoveries at Hadar and Laetoli of fossils attributed by Johanson, White, and colleagues to a new species, *Australopithecus afarensis* (see Johanson and White 1979). Additional specimens have now been added to the hypodigm (Boaz, 1988; Kimbel et al., 1994). As discussed above, two new australopithecine taxa have been recently named: *Ardipithecus ramidus* and *Australopithecus anamensis.* Figure 4 diagrams the major hypotheses that have been advanced to accomodate Pleistocene hominid fossils.

The describers of the specimens that make up most of the *A. afarensis* hypodigm, Johanson and White, consider that the fossils represent only one population of hominids and thus only one species. Many students agree with this conclusion, taking note of the fact that there was a large range of sexual dimorphism in the species (e.g. Boaz, 1988). Other researchers such as Todd Olson, Brigitte Senut, Adrienne Zihlman, Glenn Conroy, Dean Falk, and others consider that the Hadar sample contains more than one taxon. Olson's (1985) phylogeny is representative of this position: a portion of the Hadar sample represents the antecedents of the robust australopithecine lineage and another portion is ancestral to the *Homo* lineage (see Figure 4 "Split *afarensis* " phylogeny). This argument is unconvincing, at least to me, in that co-variance of traits in one or another morphological area sorts individuals into different groups, depending on the trait chosen. There are two size morphs at Hadar but it seems most reasonable to sort them into sexes.

An important paper by Radosevich et al. (1991) on the depositional environment at AL333 at Hadar bears on this argument. These researchers undertook a detailed study of the sedimentary conditions attendant to the burial of the AL333 hominids and concluded that burial had indeed been swift and at one time. The hominids had therefore been buried and probably killed by the same event. It was thus very likely that these individuals lived together as a group. Since the greatest variation in morphology at Hadar is seen within the AL333 sample, this work strengthens the argument based on morphology alone that the Hadar hominids represent one species.

A. *afarensis* is generally accorded the most basal position on the hominid lineage (Figure 4), although the earlier and more primitive *A. anamensis* may supplant it. The bonobo-like *A. ramidus* is even earlier but still uncertainly related to other australopithecines. Johanson and colleagues repudiate *A. africanus* as an intermediary between A. *afarensis* and *H. habilis,* instead postulating a million-year hypothetical direct link between *Homo* and *A. afarensis* that lacks any direct fossil documentation (see Figure 4 "Missing *Homo* Ancestor").

The early date of the "Black Skull" (KNM-WT 17000 at 2.5 my, termed by some *Australopithecus* (or *Paranthropus) aethiopicus* (from the nomen *Paraustralopithecus aethiopicus* Arambourg and Coppens 1968 based on the Omo 18 mandible), forced revisions in hypothesized ancestor-descendent relationship between *A. africanus* and the robust australopithecines. Some workers split the eastern African *A.* (or *P.*) *boisei,* derived from *aethiopicus,* and the southern African *robustus,* derived from *africanus* (see Figure 4 "Split Robust" phylogeny). Others, with whom I agree, interpret WT 17000 as an ancestral robust australopithecine at least partially coeval with *A. africanus,* which in turn is interpreted as a *Homo* ancestor (see Figure 4, "*Africanus* as *Homo* Ancestor" phylogeny). Finally, this phylogeny accepts the recently named *Homo rudolfensis* as a lineage distinct from the more gracile *H. habilis.*

SYSTEMATICS AND PHYLOGENY OF THE GENUS *HOMO*

Wood (1991) has, more than any other recent worker, pushed the notion of taxonomic and phylogenetic diversity in early *Homo* phylogeny. He has accepted the validity of *Homo ergaster* (Groves and Mazek, 1975), an early African *H. erectus* based in part on KNM-ER 1813 and ER 3733; *Homo rudolfensis* (Alexeev, 1986), a large-brained ancestor of *Homo sapiens* with KNM-ER 1470 as the type specimen; and *Homo habilis,* conceived of as small-brained and small-bodied; as all being contemporaneous early *Homo* species in eastern Africa (see Figure 4 "Split *Homo*" phylogeny). Wood's is a particularistic approach, emphasizing the morphological differences in specimens and according them significant taxonomic weight. Tobias (1991), with whom I agree, includes the specimens on which these new taxa are based all within *H. habilis.*

The uncertainty about the taxonomic unity of *Homo habilis* has also affected *Homo erectus.* The primary question is whether early African *Homo erectus,* as exemplified by crania such as KNM-ER 3733 and KNM-WT 15000 are the same species as the type specimen from Java. Some workers such as Rightmire (1990) consider that they are. Others such as Groves and Mazek (1975) and Wood (1991) consider that the early African representatives belong to a separate species, *Homo ergaster.* In phylogenetic terms the major result of this interpretation is that *H. erectus* is moved off the lineage leading to *H. sapiens.*

MITOCHONDRIAL EVE, OUT-OF-AFRICA, AND MULTIREGIONALISM

The phylogenetic history of *Homo sapiens* has become a battleground for the forces utilizing primarily molecular techniques and data, and the forces utilizing primarily morphological techniques and data. Cann (1993) has recently re-stated the "Mitochondrial Eve" hypothesis: "...all individuals alive today can trace some of their genes to a woman who lived in Africa approximately 200,000 years ago..." (p. 116). She goes on to say that this ancestor "was not our only genetic ancestor, nor was she the only woman alive at the time who may have contributed genes to modern people" (pp. 117-118).

These aspects of the mitochondrial evidence seem to have been missed by some proponents of the model of largely *in situ* evolution and regional phylogenetic contiguity, a construct termed the "Multiregional Evolution Hypothesis" or "MRE" (Frayer et al., 1993). Wolpoff (1989), for example, argues against a position that African populations would have "invaded" Europe and replaced indigenous peoples so that no local genes were passed on the succeeding generations. In fact the mitochondrial evidence does not demand this interpretation. It is important here to distinguish between lineages of genes, which the mitochondrial DNA evidence shows, and organismal lineages (Ayala, 1996).

Stringer (1989) has forcefully argued against the multiregional model, invoking primarily fossil evidence but also genetic data. He and Bräuer (1984) are the primary proponents of the "Out-of-Africa" model of modern human origins, also referred to as the "Recent African Origin Hypothesis" or "RAO" (Stringer and Bräuer, 1994. These authors point to the earlier dates of anatomically modern specimens in Africa, and to discontinuities, particularly in the Late Pleistocene of Europe between Neandertals and anatomically modern *H. sapiens*. Stringer (1989:92) notes, "I believe that the establishment of modern genes in Eurasia occurred because they were transported inside the bodies of an expanding early modern population, rather than by their gametes mixing with those of local archaic populations." Thus, there is a difference in emphasis between the Mitochondrial Eve and the RAO models, although both are more mutually compatible than is either with the MRE model.

ISSUES OF BEHAVIOR AND ECOLOGY

There has been an increasing realization that events in hominid evolution need to be understood in the context of changing environmental and ecological conditions.

Brain (1981) focused attention on the terminal Miocene event as potentially tied in to the origin of the Hominidae. Boaz and Burckle (1985) noted the trends towards globally cooler temperatures and greater amplitude of environmental fluctuations from the late Pliocene through the Pleistocene, and related these to the hominid fossil record (Figure 3). Vrba (1988) drew attention to the 2.5 ma event of global cooling and postulated that this event may have been related to the emergence of the genus *Homo*. As mentioned earlier in this paper, the paleoclimatic relationships to evolutionary changes recorded in the hominid fossil record, and whether they were gradualistic or punctuational in mode, is still debated.

The relationship of the various subspecies of *Homo sapiens* (or species of *Homo*) to ecological conditions in the Pleistocene remains clouded. But one useful construct, based on Allen's Principle, is the observation that tibia length compared to femur length is shorter in cold-adapted populations. Trinkaus (1981) showed that all Neandertals, along with extant Inuits, Lapps, and other northern Europeans, fall below a line separating them from Africans, Melanesians, and American Southwest Amerindians. The former seem to be cold-adapted populations, with relatively short distal limb segments. The fact that Skhul/Qafzeh and European Late Upper Paleolithic indices fall well above the line has been used to argue for the tropical, African origin of these populations (Stringer, 1995).

An ongoing debate relates to the degree of terrestrial versus arboreal adaptation that the earliest hominids possessed. A group centered at SUNY Stony Brook has promulgated the position that A. *afarensis*, and to some extent also *H. habilis*, were hominids that were adapted to a significant time of life in the trees (Susman et al., 1984). White and Suwa (1987) have contested this conclusion on the basis of their reading of clear terrestrial bipedal adaptations in the A. *afarensis* postcrania. Jungers (1994) and White (1994) have recently re-asserted these positions vis-a-vis the new Maka A. *afarensis* humerus from the Middle Awash. Clarke and Tobias (1995) have adduced postcranial evidence from Sterkfontein in support of a postulated arboreal climbing adaptation for *A. africanus*.

Early hominid diet remains an important area of continuing and future research. Despite the general opinion that scavenging was important in early hominid adaptation (Blumenshine, 1987) the data for this interpretation are far from ironclad.

The earliest appearance of fire in the hominid evolutionary career is also a major question. Brain and Sillen (1988) report that bones in one of the upper members (Member 3) at the Swartkrans cave site in South Africa, dating to some 0.85 ma, show evidence of burning. This is significantly earlier than the generally accepted earliest date of human fire use at Zhoukoudian, China at ca. 450 ka (Jia and Huang, 1990). The accurate dating of the first appearance of human-controlled fire is important in understanding the paleoecological context of this innovation.

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NOTE

1. The zoological family Hominidae is defined here to include members of the Superfamily Hominoidea (that grouping that includes modern apes and humans) characterized by adaptations for bipedal locomotion. Some anthropologists use the family term "Hominidae" to refer to all of the modern apes and humans, and the subfamily term "Homininae" to refer to the bipedal members of this taxonomic grouping.