

Roots and Branches:
Hominid Evolution in a Macroevolutionary Perspective

Greg Laden
Department of Anthropology
University of Minnesota

Introduction

Since the discovery of *Australopithecus* nearly 80 years ago (Dart 1925), there have been many additions to, and occasional removals from, the hominid fossil record. Correspondingly, the apparent pattern of hominid evolution, as well as explanations for that pattern, also changed (Foley 2002). The prevailing historical descriptions of human evolution are closely linked to the nature of the fossil record as it is perceived at any one moment in time. For example, Darwin, (1874) in the virtual absence of any relevant fossil record, conceptualized human evolution as co-evolving changes in stature, locomotion, form and utility of the hands, use of technology, and enlargement of the brain. Today we know that upright posture and bipedalism evolved far earlier than the use of stone tools or a large brain, decoupling these quintessential human traits (Lovejoy 1988). Similarly, a unilineal, sometimes gradualistic view of human evolution, in which each newly discovered species is presumed (or forced, if necessary) to fit as a link in a simple chain from primordial ape to modern human has given sway to an understanding of species-level diversity of early hominids. It is now clear that many distinct species arose, diversified, and became extinct, and it is not at all clear which of several species may be on a strictly defined “human lineage.” The precise genealogy of living *Homo sapiens* now shares its place among equally compelling such as the adaptation of early hominids to novel habitats; the diversity (number of species), disparity (range of differences among species) and geographic range of early hominids; and the relationship between the fossil record and the pattern of genetic distances between the living apes (Ruvolo and Pilbeam 1986).

Evolutionary process and pattern are distinct concepts, the former roughly equal to cause, the latter to consequence. The pattern of hominid evolution must be closely linked to the process by which it occurred, and thus, understanding the pattern may be a critically important step in understanding the process. As mentioned, there cannot be a close linkage between bipedalism and the use of chipped stone tools, because the former arose millions of years before the latter. This does not mean that there is not a functional connection. Perhaps lithic technology would be unlikely in a quadruped, and the evolution of this behavior was made possible by an earlier event, but, the same can be said of the origin of limbs hundreds of millions of years ago.

Clearly, any hypothesis that directly links bipedalism to lithic technology (or large brains or any other later event) is falsified by the documented pattern of the hominid fossil record.

From the late 1970s through the early 1990s, numerous hominid fossil finds, the identification of several distinct species, and the more accurate dating of fossil deposits resulted in a rich record of hominid evolution for the period of about 3.2 to 1.5 million years ago. A suite of traits associated with several different hominid species became apparent, including a form of bipedalism different from modern humans, megadonty and thick enamel associated with large chewing muscles, and the use of lithic technology by 2.6 mya (Semaw 2000). However, almost every researcher working in African palaeontology has recognized that the description of the pattern of early hominid evolution was in part shaped by vagaries of the fossil record, owing to biases in where research was carried out, what was preserved, and possibly also the order in which fossils were found.

Gaps and other biases in the fossil record have and always will obscure the exact temporal pattern of early hominid evolution, but in recent decades the fossil record has matured significantly. It may now be possible to newly characterize the hominid fossil record – to revise our description of the pattern of hominid evolution – in a way that would suggest a revision in how we understand the process of that evolution. While recent discoveries in the time period prior to 3.0 million years continue to show diversity and physical variation in hominids, there are differences in the earlier material. Prior to 3.0 million years, there are no individuals with extreme megadonty such as in later *Paranthropus*, or enlarged brain cases as in several later hominids, and no evidence of chipped stone technology, despite a great deal of searching. Bipedality in at least some of the earlier hominids may have been different than for the later, post 3.0 mya australopithecines. There is now a growing list of well-scoured deposits that contain few or no hominid fossils, suggesting limitations of geographical range before 3.0 mya (Harrison and Baker 1997; Walker 2002) In sum, it seems that earlier hominids are adaptively different, less diverse and less disparate, and more geographically restricted than later hominids. Finally, the most recent finds of 6 to 7 mya hominids in Chad suggest that the antiquity of hominids is at the older end of the range most recently estimated on the basis of DNA studies.

These observations may allow the pattern of hominid evolution prior to about 1.5 mya to be described as having two phases:

Phase I: The initial separation of a population of early hominids from a chimpanzee-like last common ancestor (LCA) somewhere around 6 or 7 million years ago followed by about 3 to 4 million years of low species diversity and primarily phyletic evolution. This initial rise of hominids involved novel dietary and locomotory or positional adaptations, but these changes were relatively small in magnitude. It may be possible to consider these earliest hominids to have been one of a variety of chimpanzee-like forms, with a somewhat different (perhaps moderately specialized) diet and different but overlapping habitat preference, and otherwise not extraordinary.

Phase II: Between roughly 3.2 and 2 – 1.5 million years ago, hominids underwent a species radiation involving a diversification of dietary and habitat preferences, varying degrees of encephalization, varying degrees of increase in molar size, and changes in technology, distributed unevenly among the genera *Australopithecus*, *Paranthropus*, and *Homo*.

A key feature of this model is the interpretive importance of an adaptive radiation and geographical spread that define Phase II *vis-a-vis* the lack of these events (as known so far) for Phase I. Major evolutionary events often lead to changes in evolutionary pattern, such as a radiation of species or the increased range of one or more related species. A fossil record with a long period of relative stasis followed by a rapid increase in the number of species (increased diversity) and a diversification of forms (increased disparity) indicates that something evolutionarily important happened at the beginning of, *and throughout*, that period of diversification. Extinction events or climate change may have opened up opportunities or caused speciation by breaking a larger population into smaller, separate ones, or an adaptation may have emerged that allowed the invasion of niches previously unoccupied by the taxon in question, as has been theorized and described in detail by Vrba and others (Bromage and Schrenk 1995b; Vrba 1995b; Vrba 1996b; Vrba 1999)

The converse may be true, but this is less clear. If a radiation of species does not happen, does this mean that nothing of evolutionary significance has happened? It is an increasingly common view among paleontologists that a very large percentage of the living species of

vertebrates arose during radiation events (Schluter 2000; Stanley 1979; Stanley 1992).

Therefore, on average, one might bet on the association of radiations and important evolutionary change, and bet against the association of gradual or minimal taxonomic novelty and important evolutionary events. However, this is not a safe bet on a case-by-case basis. For example, it appears that the number of species of hominids that existed simultaneously from about 1.5 million years ago to the present was never more than two or three, at times possibly only one, and that there were perhaps no radiation events during this period, yet the differences between the genus *Homo* at 1.5 mya and the present are significant. It might be safest to say that important evolutionary changes need not be dramatic radiations, but a dramatic radiation is likely an indicator that something important has happened.

An important implication of this model is that the Phase I pattern might have resulted from a single process, and not a series of different events or causes. The rise of *Paranthropus* and the rise of *Homo*, extreme megadonty, increased brain size, the use of stone tools, increased geographic range and “modern” locomotory pattern all occur during this period. All previous macroevolutionary models (Foley 2002; McHenry 1994; Stanley 1979; Vrba 1999) describe this period as a *collection* or *series* of events each with a specific (climatic) cause and each accounting for a different aspect of the mosaic of hominid traits characteristic of this time period. Here I propose a contrasting model, which is to think of Phase II as a single radiation event, whereby all of these traits may be viewed as part and parcel of the same process, sometimes having different effects among the species that arose during this time.

It is possible to characterize “macroevolution” as the study of patterns in the fossil record, independently of the actual process (causes and consequences) of evolution at the finer scale. However, it may also be possible to connect macroevolutionary patterns to finer evolutionary process, thus connecting historical events to biological function. This is in large part the idea behind the concept of an *adaptive* radiation. Here, I argue for a slightly revised way of thinking about adaptive radiations, and as well I argue that Phase II hominid evolution was such an event. Prior efforts to link specific climatic events with specific happenings in hominid history have, I will argue, overshoot the mark with respect to specificity. Perhaps the best way to characterize Phase II hominid evolution is as a period when certain conditions relevant to hominid evolution became more likely true, even if cyclically (or at least discontinuously) so.

This resulted in a series of “evolutionary opportunities” that were sometimes converted into evolutionary events by the contingent overlap of niche, population, and luck, and sometimes not.

In this paper, I summarize and present in various formats the currently available hominid fossil record, assess this record for accuracy and completeness, and compare it to expectations from macroevolutionary theory to see if it is reasonable to describe at least part of this record as an adaptive radiation. Following on earlier work (Hatley and Kappleman, Vrba, Others, Laden and Wrangham), I find that it is possible to characterize much of the Pliocene and Early Pleistocene fossil record as a single, large-scale evolutionary event. From this perspective it is interesting and informative to review the nature of change in views of the hominid fossil record.

Emergence of a better fossil record

Our concept of the hominid fossil record in time and space influences our understanding of human evolution, and almost certainly, views of human evolution have biased interpretations of that record. Reviews of the history of thought about the hominid record relevant to the present discussion can be found in several places (Foley 2002; Lovejoy 1988; Stanley 1979) Already mentioned is Darwin’s co-evolutionary story of technology, bipedalism, and brain evolution. As the relationship between bipedalism, technology, and large brains became decoupled, additional considerations have been brought into the discussion of hominid evolution. Hunting has always been considered important in human evolution but when, where, and whether or not there would have necessarily been a pre-hunting “scavenging” phase have all been debated. The presumed movement from forest to woodland or savanna to grasslands has been linked to bipedalism in several ways, including: selection for increased vigilance (an upright ape can see a predator or prey); efficiency in locomotion (following herds, or moving between increasingly rare patches of woodland and forest); and upright stature freeing the hands to advance technology especially in regards to hunting and carrying objects across the greater distances between resources or safe areas on the expanding African savanna.

Dietary (e.g. (Kay 1981)) and social (e.g.(Lovejoy 1981)) hypotheses, and hypotheses that combine the two (root-digging grandmothers (Hawkes, et al. 1997) and root eating chimps

(Laden and Wrangham in press?) or root cooking *homo* (Wrangham, et al. 1999)) now compete to explain critical stages in hominid evolution. It is appropriate that dietary hypotheses be central to the discussion of hominid evolution. Although a great deal is made of the importance of bipedalism, early Australopithecines were not bipeds in the same way as Middle and Late Pleistocene *Homo*, but the masticatory adaptations of australopithecines are, compared to other primates, extreme, perhaps even shockingly so. Megadonty and the associated enhancement of masticatory musculature in hominids is so striking that it is very tempting, and probably at least partly correct, to believe that this dietary adaptation explains a great deal about the evolution of hominids.

Until the mid or late 1980s, the hominid fossil record predating 3.5 mya or so consisted of only a few scraps. Estimates from molecular study placed the time of divergence of chimpanzee and human lineages from a last common ancestor (LCA) between two and four million years *before* the earliest well documented fossil record (Ruvolo 1997; Ruvolo, et al. 1991; Ruvolo and Pilbeam 1986; Wrangham and Pilbeam 2001). It had become apparent that what I call Phase II hominids were diverse, and it was not known if this diversity existed during the murky late Miocene (Phase I). In subsequent years, several new finds were made, and the fossil record for this earlier period has been significantly increased. In this regard it is interesting to selectively review comments by the researchers knowledgeable of this fossil record. In 1998, M. Leakey et al note regarding new *Australopithecus anamensis* finds that:

One explanation for the hominid fossil record from nearly 4.5 Myr to just later than 3 Myr is that it represents one single, evolving species ... An alternative explanation is that the three recognized taxa indicate some bushiness in the early hominid tree. (Leakey, et al. 1998)

And later, while erecting the new genus *Kenyanthropus*, an overlapping team of researchers note:

The eastern African hominin record between 4 and 3 Myr is represented exclusively by a single species, *A. afarensis*, and its possible ancestor, *Australopithecus anamensis*, which are commonly thought to belong to the lineage ancestral to all later hominins. This apparent lack of diversity in the middle Pliocene contrasts markedly with the increasingly bushy phylogeny evident in the latter hominin fossil record... New hominin discoveries ... indicate that multiple species existed between 3.5 and 3.0 Myr. (Leakey, et al. 2001a)

One detects in these and similar comments uncertainty about species diversity in the ever-narrowing time gap between 3 mya and the presumed LCA a few million years earlier, and at the same time recognition of a clustering of adaptive speciation in the later, post 3 mya period. With the recent discovery of very early australopithecine material from Chad (Brunet et al 2002), it may be that a relatively early date for the chimp-human split may be reasonable, thus increasing the time frame between the LCA and a later Pliocene radiation of forms (assuming for the present discussion that this find will become accepted as an early member of the hominid group). This hominid find also supports, as pointed out by Wood (2002), the idea of early diversification of australopithecines, and more importantly, the viability of evolutionary models that involve homoplasy and sequential adaptive radiations. Nonetheless, as will be discussed below, there is very little evidence of significant diversification prior to 3.0 mya.

The presence of early hominids in Chad is important for understanding the geographical spread of hominids, and the same is true of the later aged hominid originally reported as *Australopithecus bahralghazali* in the same region (Brunet, et al. 1995)a. Nonetheless, Late Miocene deposits at Mananga (Tanzania)(Harrison 1997), Sahabi (Lybia) (White 1983), Langebaanweg (South Africa)(Singer 1961) and see summaries in (Bromage and Schrenk 1999), and the Western Rift (Congo and Uganda) (eg (Boaz, et al. 1992) lack hominids, and at Baringo (Kenya), extensive exposures have produced very little (Hill 1985; Kingston, et al. 2002; Senut, et al. 2001; Ward and Hill 1987). Increasingly, the fossil record of the late Miocene indicates that there are regions and habitats where hominids were not present or at least not common (Leakey 1999). It is reasonable to hypothesize that the geographical range and species diversity of hominids prior to ca 3.0 million years was much less than after that time.

As a first step in understanding hominid evolution in a macro-evolutionary perspective, I provide two lists of hominid species, in Table 1. Based on the same source data, one list is meant to maximize apparent species diversity, in order to overestimate rather than underestimate the number of first appearances, species at one point in time, or possible extinction events, in assessing the overall pattern of cladogenesis. The second list is meant to reduce the appearance of variation, by combining similar forms, or sinking previously questioned species into other forms. Since only similar forms are combined in the second, reduced variability list, there it

better represents phenotypic diversity (rather than species diversity), or, “disparity,” of the fossil record.

Table 1a lists the African hominid species of the Miocene through the Middle Pleistocene that are found in today’s fossil hominid literature. The first and last appearances are the earliest and latest begin and end range, respectively, among the known localities at which these hominids are found. These localities are listed in the Appendix. The specific dates for each locality are taken from a wide range of sources (as indicated in the Appendix) and in some cases are interpolated or extrapolated from various sources in the literature, but interestingly, few if any of these dates are likely to be controversial, owing to the impressive work done by a wide range of researchers. (This is not to say that these ranges will not change with further research, only that the geological contexts are much better understood than a decade or two ago.) The midpoints are interpolations of the first and last appearance dates.

If the ages of the localities from which these hominids are found are surprisingly but pleasantly uncontroversial, then what is possibly controversial are the species listed in Table 1a. Among the australopithecines, I have listed all of the different species that have been proposed but not recently re-sunk into earlier types, with the exception of *A. crassidens* (a paranthropine from South Africa) and *A. bahrelghazali*. The former is a name given to several *Australopithecus* or *Paranthropus robustus* like bones, and more lately given to a smaller subset of similar fossils. The latter is a species erected for finds in Chad but more recently questioned (Brunet, et al. 1995). I use these two “species” in Table 1a because I am less concerned with the specific agreement over each of these species as I am with diversity in the record. If these sets of fossils are different enough from previously known forms for intelligent and well respected scholars to assert their species status even if just temporarily, then it is fair that a list of hominids meant to show the greatest diversity would include them provisionally.

As for early *Homo*, the situation is of course much more difficult. Most likely, early homo (*H. habilis*, *H. rudolphensis*, etc.) represents a small number of very disparate species, and possibly a population caught in the act, as it were, of rapid evolution. It may be that in the long run no current concept of species, living or fossil, would ever be able to clearly accommodate such a population, if in fact we are seeing dynamic change over a few hundred thousand years of time. Nonetheless, paleoanthropologists are required by an unwritten commitment to taxonomy

to place all fossils eventually in a species, and for the present purposes I have adopted one version of many possible ones to represent this part of the genus.

Table 1b is derived from Table 1a. Here, I have combined several of the early, East African gracile australopithecines into a single group. This group is not meant to indicate that they are all of one species, but rather, following others, to suggest that some or all of these species reflect phyletic evolution of a single species or population (Leakey, et al. 1998; Leakey, et al. 2001a; Leakey, et al. 2001b; Ward, et al. 2001). Also in Table 1b, I have adjusted the dates of *Homo ergaster* to include the overall dates for *H. ergaster/erectus*, in recognition of the likely fact that they are the same species, and to account for the global Old World distribution of *H. ergaster/erectus*. Similarly, Table 1b has an adjusted date for *H. sapiens*, dropping the earlier robust forms (assuming them to be transitional between *H. ergaster* and *H. sapiens*, and thus in either or both categories) and extending *H. sapiens* to the present (for which there is circumstantial evidence).

With these changes, Table 1b represents a simplified list, intentionally reducing the appearance of variation in the earlier and later periods, thus providing the basis for graphical representation of my model, biases intentionally included for effect. Note that most of the analyses done here use the diversity-biased Table 1a, while the comparative graphics used below use the personalized biased version in Table 1b.

Figure 1, based on Table 1a, is a schematic representation of the currently known and reported fossil record for African hominids from the Late Miocene through the Middle Pleistocene. Approximately one third of these species were unrecognized prior to 1990, and only about one third were known in 1970. Of the nearly 150 localities reported in the literature from which this representation is culled, only a few were known and reported by 1970, and perhaps half have been reported since the late 1980s. Of those 150 localities ranging in time from about 7 million years ago to the middle Pleistocene, perhaps 20% do not have evidence for hominid activity (fossils or stone tools). This is in contrast to the 1970s and 1980s when most of the reported sites, dating to after 3.5 mya, were associated with such evidence (a bias likely caused by interest in specific areas because of the presence of hominids).

Figure 2 depicts the density of sample localities used in this study over time. The larger (pink) line is drawn by plotting the geological age (midpoint) for each sampling locality against the rank order of age. If the distribution of localities over time was even, this would be a very

straight line. Unevenness of sampling (i.e., under-sampling) causes the line to be curved or kinky. The blue line depicts the density over time of sample localities that yield hominid remains. By comparing these two lines, it is possible to visually (and intuitively) assess a) the temporal limits of hominid samples, and something of the pattern of hominid presence or absence in the geological record over time, and b) the likelihood that any patterns observed in the hominid record are a function of the nature of the geological record itself, i.e., biases due to under-sampling in certain time periods.

The red line in Figure 2 depicts the distribution of midpoints of known hominid species (using the longer list from Table 1a). This line shows that the presence of hominids species, and thus likely their emergence (speciation) and/or extinction, is not uniform over time. The nature of this pattern is discussed at length below. The point I wish to make now is simply that it is likely that the patterning we observe in the distribution of fossil hominid *species* over time is not likely to be the result of biases in the record of hominid *fossils* over time, which in turn, is not likely to be the result of major biases in the distribution of fossil *sites* over time, at least for the period from about 4.5 mya to recent times. Although the same cannot be said for the period of 4.5 to 7.0 mya, it is notable that there are numerous fossil sites from that period, and that larger scale patterns, such as the overall distribution of species geographically and the disparity or diversity of hominid forms, can be reasonably albeit provisionally estimated for that earlier period.

Figure 3 compares a series of previously reported depictions of hominid evolution, recreated using the same phyogeny-free approach I've used elsewhere in this paper. I have selected these representations because they show a wide range of different conceptions of hominid evolution over the last 30 years, not as a means of a criticism of any given representation. In fact, each of these representations served well its initial purpose. A version of Figure 1 (from data in Table 1a) is replicated on the composite Figure 3 for comparison, as well as a representation of the pruned species list from Table 1b. What is notable about this figure is that the current representation, which is what I believe to be an honest representation of the currently available dataset that has resulted from the hard work of a large number of dedicated workers over several decades, is a) the best we can do today because it has more data, more accurately and fully reported, compared to any earlier conception of hominid evolution; b) very believable because the available dataset has finally matured to a degree that it is possible to

concern ourselves more with patterns in the record than with biases in the record (after about 4.5 mya) and c) *very different from most or all earlier conceptions of hominid evolution* in some very important and interesting respects.

Phase II hominid evolution as depicted in Figure 1 and Figure 3d and 3e could be characterized as a single evolutionary event in which a time period characterized by low species diversity of gracile australopithecine forms gives way to a major, complex, and mildly protracted radiation of forms, having led by just under 2 million years ago to the rise (and in many cases extinction) of several species of australopithecines, paranthropines, and early versions of *Homo*, with a diverse set of locomotary, dietary, and technological adaptations.

Adaptive or Species Radiation in Relation to Hominid Evolution

I propose that the pattern of hominid evolution in the Late Miocene through the Pliocene, as we can describe it from the currently available fossil record, was a single species radiation. This evolutionary “event” was not a series of radiations associated with different climatic changes as has been proposed by others, most recently Foley (Foley 2002), but rather, accords well with the simpler model of a *single* if somewhat protracted radiation. Radiations are typically thought of “adaptive radiations” whereby a diversity a founding taxon spreads into a wide range of differing habitats. Here, I propose that while this may be true, it is also true that an adaptive radiation can consist of a diversification of forms within a more narrowly defined set of related adaptations, with some or even much of the diversity representing different degrees of specialization, different modes of adaptation to a similar habitat, and the rise of adaptations that expand the range of possible habitats in which a taxon may be found. More accurately, it may be understood that the disparate phenotypic clues to adaptation that we see in the fossil record can be manifestations of a set of variant solutions to a narrower set of ecological potentials or constraints. For example, the use of stone pounding tools, fire, and large teeth (megadonty) could be thought of as three ways to solve the same problem of hard to eat, lower quality or tough food. Thus, the diversity of adaptations in a given adaptive radiation need not be independent from one another, and can be linked functionally, historically, and ecologically.

It could be said that the history of life, at least vertebrate life, is best modeled as a collection of adaptive radiations, and this process of increasing diversification of life is fundamental to Darwin's conception of evolution (see Mayr 1991: 36; Stanley 1998:65). However, exactly what an adaptive radiation is, how it works, and how an *adaptive* radiation may differ from a radiation that is not adaptive is a matter of discussion and debate. Mayr defines adaptive radiation as "Evolutionary divergence of members of a single phyletic line into different niches or adaptive zone." (Mayr 2001:283). Simpson, accredited with the recognition and initial exploration of this theoretical concept, also notes that adaptive divergence can lead to change in the ecology that alters the diversity of niches into which evolution can occur, thus suggesting a dynamic interaction between the niches and the niche-fillers, over long time periods (eg Simpson 1949: 117). However, Simpson's definition and Mayr's are essentially the same, and as noted by Schluter, incorporate "two core [essential] processes... a rise in the rate of appearance of new species and a concurrent increase in ecological and phenotypic diversity," (2000:10).

A simple alternative to adaptive radiation is "nonadaptive radiation," which is the diversification of species absent ecologically relevant adaptations. For example, diversification of species because of reproductive isolation arising from geographical barriers, or mating barriers owing to sexual selection, would produce multiple species via a mechanism that has little or nothing to do with ecology (see discussion in Schuller 2000 for examples such as fruit flies and snails).

It is not clear, however, that these two processes are necessarily distinct or that they do not interact. Through mechanisms such as those suggested by Simpson and expanded on especially by Vrba (Vrba 1982; Vrba 1988; Vrba 1985; Vrba 1988b; Vrba 1995a; Vrba 1995b; Vrba 1996a; Vrba 1996b; Vrba 1999) and others, or through simple divergence of niches under conditions of climatic change, one can easily imagine ecological and non-ecological processes together giving rise to a multitude of species and subspecies. Indeed, it may be the case that speciation itself is much more likely under conditions of reproductive isolation through either geographical separation or sexual selection, so that adaptive diversification would be unlikely to occur at all if non-adaptive isolating mechanisms were not in play. Furthermore, once adaptive divergence occurs subsequent genetic interaction between reunited populations would be

reduced, and species recognition mechanisms may keep nascent species separate while both re-converge on ecological niches that are becoming more similar to each other with climate change.

Hominid evolution is interesting in this sense, if only one or two major morphological changes – such as bipedalism and megadonty – are considered the essential characteristics of the many species of Pliocene hominids. Perhaps this diversification was caused by geographical isolation under climate change, through vicariance and Vrba's habitat theory that also caused the rise of novel niches and thus selected for novel ecological adaptations. The result may have been a series of species that are distinct not because of distinctly different ecologies, but rather, because of different degrees or intensities of a similar ecological adaptation, with further diversity added because of geographical effects.

I propose that it is reasonable to hypothesize that hominid evolution in the Late Miocene and Pliocene is an adaptive radiation because diversification is associated with novel adaptations that are minimally of different degrees in different forms (i.e. megadonty in australopithecines, and super-megadonty in paranthropines), and because the total adaptive suite of hominids of this time periods probably involves several different traits that are not evenly distributed among the known species (including tool use and encephalization).

In defining and settling on criteria to describe and test for adaptive radiation as a phenomenon related to any particular taxon, several issues arise that impact on how we think about hominid evolution. It may be said that the entire structure of vertebrate life is a nested hierarchy of adaptive radiations, but adaptive radiations at lower taxonomic levels constitute the fundamental form of this phenomenon, following Darwin's fundamental principle of descent from common ancestry (which unambiguously applies to vertebrates). Hominids as a group, and Miocene/Pliocene hominids in particular, clearly qualify as a lower level taxon, at which the dynamics and results of adaptive radiation can be studied, or conversely, to which adaptive radiation theory can be applied.

The timing of adaptive radiations is another consideration. Simpson used the term "nearly simultaneous" in speaking of adaptive radiations, but a geologist's "simultaneous" may be a very protracted period for an archaeologist or a hominid looking for a meal or a mate. The realization over the last 30 years that climate cycles can be "geologically" quick, with Milankovitch cycles running at phases of ca 120 thousand years and ca 40 thousand years, has led to consideration that climatic change leads to speciation or extinction at rates that are too

fast to be observed in the fossil record: It is possible that rapid climatic change, especially Milankovitch scale change greatly amplified during the Pleistocene, compresses evolutionary events to below geologically visibility. Along this line of thought, one might expect that a particular adaptive radiation, in order to be considered as a single, unified event, would have to occur during one of these short cycles.

If this is so, then we would expect that the fossil or genetic evidence associated with specific, well-understood adaptive radiations tend to indicate diversification of species as each having occurred in a geological instant, ideally corresponding to a single Milankovitch cycle. To explore this idea, I've assembled data from several documented and reported species radiations (Table 2). For each example, either fossil or genetic evidence is used to estimate the duration of the radiation. The duration is the time period from the first splitting of species to the last splitting of species, and in each case, the estimate is conservative, excluding rare early or recent splits, and focusing on the time period during which most but not necessarily all of the speciation events are likely to have occurred. The range of durations for adaptive radiations is large, from those short enough to have occurred during a single Malaknovitch cycle to well over 2.5 million years. This data set is not sufficient to characterize adaptive radiations in general, but it clearly suggests that phenomena classified as adaptive radiations do occur across many Malaknovitch cycles.

Although this may seem surprising, it really should not be. It seems very likely that once a taxon possessing the traits that are potentially useful in a particular niche exists, or once a novel niche arises, that two opposing aspects of a complex dynamic would be true. First, the number of possible "opportunities" for speciation is very large, with many different geographical areas interacting with many different populations, resulting in a wide range of possible niche-incursions each with a unique set of competitors and other factors. Indeed, it is surprising from this perspective that adaptive radiations tend to lead to so few species (i.e., dozens or fewer). Second is the extreme unlikelihood of any particular speciation event either happening to begin with, or being sustained against the multiple forces of extinction or re-absorption into parent populations. It is likely that the interplay between strong forces leading towards speciation and strong forces working against it would lead (in the context of historical contingency) to a pattern in which periods of homeostasis in species diversity would interdigitate (in the fossil record) with periods of frequent diversification.

That a major radiation would occur across a series of major climatic swings seems, from this perspective, exactly what one would expect. When it comes to adaptive evolution, it is not true that opportunity knocks once. Climatic cycling accentuated over the last several million years would produce repeated, but in some ways distinct, opportunities for both speciation and extinction.

Another phenomenon related to adaptive radiation, which supports my assertion that adaptive and non-adaptive processes often, perhaps invariably, work together, is parallel evolution. This is seen, for example, in the adaptive radiation of freshwater fish species in previously glaciated temperate regions. The geographical isolation of founder populations in a multitude of lakes leads to repeated evolution of similar adaptations. Thus, the radiation is adaptive because the rise of new species involves the entry into and adaptation to novel niches, but it is nonadaptive because the total number of species and subspecies is in large part a function of geographical isolation and effects of historical contingency. The ultimate result is that many instances of homoplasy occur.

Hominid Evolution in light of Adaptive Radiation Theory

That hominid evolution involves adaptive radiation has been proposed earlier, by several researchers as outlined above. (Below, I will contrast the present model with the most recently proposed and possibly richest models by Foley and Vrba.)

How do the salient aspects of adaptive radiation (or species radiation in general) relate to hominid evolution? First, I would like to summarize some of the key aspects of adaptive radiations:

- 1) Duration may be short (“geologically instantaneous”) to longer, up to 2 or 3 million years.
- 2) A diversity of adaptations among the resultant species should be observed.
- 3) Parallel adaptations, representing multiple similar but geographically distinct speciation events, may be observed.

- 4) A correlation between habitat change and the radiation event should be observed, the former presumed from climatic change shown by roughly coeval changes in other taxa and climate proxy indicators.

These points along with the presumption of common ancestry are in accord with Schluter's conception of testing for adaptive radiations (Schluter 2000:10-21).

Phase I hominid evolution involved modest alterations from a presumed chimpanzee-like ancestor, no clear radiation, and no major increase in geographical range. Indeed, as it is known so far, the geographical range of these hominids may have been much smaller than the recent range for chimpanzees, in terms of total land area. If significant adaptive evolution is typically associated with adaptive radiation and expansion of geographical range, then these early modest developments in the earliest hominids were not too significant. In retrospect, one might even say that early hominids were simply a form of chimp, a bit odd for a chimp, and possessing, to use an old-fashioned but entirely correct term, preadaptations that would later become part of another evolutionary story entirely. The real divergence from a chimpanzee like form was not to occur until later.

The modest initial diversity seen in the fossil record, including a small number of gracile australopiths, may represent the kind of variation we see today among the subspecies of chimpanzees, accentuated by temporal factors that are likely to add apparent variation to fossil species that never existed coevally among the living species, and further accentuated by intensive work in particular regions. The Phase II radiation of forms may begin about the time that early robust forms of Australopith emerge, between 2.5 and 3.0 mya. Novel species seem to appear until close to or just after 2.0 mya. Thus, the radiation as a whole lasts either about 1.2 million years (3.1 – 1.8 mya?) or less than a million years (ca 2.6 – 1.9 mya). Either way, the total length of time is not great for an adaptive radiation in a vertebrate species.

Figure 4 is a schematic depiction of different ways in which the pattern of hominid evolution has been viewed in contrast to what is being proposed here. Figure 4a simply represents the ape lineage as distinct from the human lineage, with the presumption that unique human traits (bipedalism, freed hands, technology, large brains, etc.) co-evolved. Figure 4b shows what is essentially the currently held view. Bonobos have been brought into the picture in recent years, some researchers suggesting that they represent the range of variation of potential

hominid/pan ancestors, others (e.g. Wrangham, Wrangham and Pilbeam) suggesting that bonobos are derived from a chimp-like form. In this conception (Figure 4b), there are two major steps in hominid evolution, an earlier one giving rise to a diversity of australopithecines (along the first half of the hominid lineag) and the second giving rise to unique traits of the genus *Homo*, including a large brain and more advanced technology.

The third representation, Figure 4c, is what is being suggested here. There are three significant differences in this way of looking at things compared to previous thinking. First, all early hominids prior to the Phase II adaptive radiation are placed together with chimps, bonobos, the chimp-bonobo LCA and the chimp-human LCA and all other possible players (known and unknown) into the broadly defined category of “chimp-like” forms. Second, in order to allow this to be reasonable, the defintion of “chimp-like” is expanded, but only a little, to accommodate the range of variation seen across living chimps and bonobos, and assumed for extinct early Australopithecines. Third, the adaptive radiation about half way between the chimp-human LCA and present day humans is identified as the key “moment” in hominid evolution.

Figure 5 shows a representation of this adaptive radiation in relation to a few key climatic events, other species radiations, and the hominid stone tool record. If the shorter, later version of the Phase Two adaptive radiation pertains, then it is interesting to note that robust australopithecines, *homo*, and the first known use of lithic technology, are all virtually simultaneous. Along with these changes there may also have been increases (and decreases?) in brain size. And, of course, near the end of this time period, and possibly after this radiation is technically over, there arose a much larger brained form (*Homo ergaster/erectus*) and new lithic technologies (Acheulean). Whether or not *H. ergaster/erectus* and the Acheulean (which are likely linked to each other) is part of this radiation or a later phenomenon can be debated, but it should be noted that following the emergence of this latest early Pleistocene hominid, the extinctions of other forms seems to be fairly common. This could indicate that *H. erectus* out competed the other hominids (the preferred model for those with a flare for the dramatic) or that *H. erectus* was somehow better suited to survive in an increasingly arid (or otherwise inhospitable) climate that was not suitable for the other hominids (my preference).

The Phase II evolution of hominids was of a duration well within the expectable time range for a typical species radiation. The effect was the rise of a diverse range of adaptations, though with some commonality among them. There may have been parallel adaptations, as has

been suggested for multiple instance of encephalization (Collard and Wood 2001; Lieberman, et al. 1988; Lieberman, et al. 1996; Wood 1985; Wood 1992) and possibly robust forms (Grine 1988; Walker 2002; White, et al. 1981). The entire event is correlated with a series of climate swings that signaled the onset of the Pleistocene (Bromage and Schrenk 1995b; Bromage and Schrenk 1999; Pickford 1991; Stanley 1992; Vrba 1988a; Vrba 1989; Vrba 1985; Vrba 1988b; Vrba 1995b; Vrba 1996b; Vrba 1999). Overall, there is nothing very different about this evolutionary event than one would expect for an adaptive radiation.

The most important outcome of this way of thinking is that efforts to either associate a particular point in this event (i.e., the onset of it) with a particular climatic event, or to match minute details within this event (i.e. the first stone tools vs. the first robust forms, etc.) to specific climate events may be not only futile but also unnecessary. It may be best to think of the ca 3 – 2 mya period as a roughly correlated set of adaptive changes in hominids and climate shifts in Africa. For the hominid lineage, the Late Miocene, through the Pliocene consisted of a series of opportunities afforded to a variety of populations, some in the “right” place at the right time, some not, resulting in the chaotic and internally indiscernible and unorganized pattern that is typical of this sort of phenomenon.

How is the present model different from or similar to that proposed earlier by Robert Foley (Foley 2002) or the extensive work by Vrba ((Vrba 1996a; Vrba 1999)? First, I attempt here to analyze species diversity or disparity within hominids without making assumptions about the taxonomic relationships among the forms available. This eliminates any possibility of describing specific adaptive or phylogenetic histories (and thus, Foley’s model is more informative, although his also has greater risks of being wrong in more places). Second, I am explicitly indicating that Phase I evolution of hominids was, so far as the fossil record shows at present, not known to have been an adaptive radiation. This does not rule out the possibility that there was one, but given the advances in the quality of the record together with what seems like a greater preponderance of no-hominid or few-hominid fossil bearing deposits for Phase I than for Phase II, argues against a Phase I radiation. Third and most importantly, these two models differ in that Foley suggests either 3 or 4 different radiations for what I call Phase II (depending on whether Foley’s 5b is in my Phase II or not), while the present model conflates all these radiations into one. In comparing the two models, it might be the case that Foley’s model provides superior nuances and details to the description and interpretation of the hominid fossil

record, but at the same time, has greater risk of being wrong in more places, and it may overlook functional or adaptive connections between different phenotypic manifestations. The present model, by contrast, specifically and uniquely asserts that dietary and technological shifts across this range of adaptations are different faces of the same adaptive coin. It is important to note that Foley proposes 7 radiations, the earliest (bipedalism) and latter-day adaptations (projectiles and expanded use of aquatic resources) being unrelated to my proposed Phase II radiation.

With respect to Vrba's work, the present idea is actually very similar in that Vrba's toolkit of models involves the coming and going of conditions of speciation. However, it seems that in all of Vrba's work, the linkage between specific climatic events and specific adaptations pervades, as with Foley. In addition, as I discuss below, I believe that the temporal shape of the Phase II hominid radiation is distinctly different than that for bovids, with the former beginning earlier.

Causes, consequences, and correlations

Relating hominid evolution, or the rise of any particular species, to climate change has been the objective of numerous studies such as those by Vrba (Vrba 1988a; Vrba 1985; Vrba 1988b; Vrba 1995b; Vrba 1996b) and others (Brain 1995; Bromage and Schrenk 1995b; Bromage and Schrenk 1999; Foley 1994; Kimbel 1995; Pickford 1991; Rightmire 1995; Roberts 1981; Ruff 1991; Stanley 1992; White 1995). This is reasonable, because major climate change is likely to change the nature and distribution of important hominid habitats, *and* to affect the biogeography of hominid populations. Either, or more likely, both of these working together, would result in an increased chance of a speciation event. However, despite the fact that a major climate change very close to 2.6 million years ago is increasingly evident, and frequently if only provisionally shown to be associated with specific events in hominid evolution, it is hard to ignore the diversification of australopithecines prior to this date, as well as after. In other words, if there was an adaptive radiation that involved speciation events distributed, even if unevenly, over a million years of time, then there is only a limited amount of explanatory power in a given climate change (presumably one especially intense Milankovitch cycle). There is no doubt that

one or perhaps a few major climate events during the Pliocene and perhaps the early Pleistocene were of special importance in hominid evolution, perhaps effecting both speciation and extinction. However, any such landmark events may be better understood in the broader context of a ca. 1 million year long period of transition from more forested and wooded conditions to the Early Pleistocene conditions of increased seasonality, decreased wetness, and the spread of woodland and grassland at the expense of more closed environments.

Nonetheless, unifying explanations are tempting and even comforting, so even if we cannot have a single climatic *event* to explain hominid evolution, we can still think in terms of powerful adaptations related to climatic trends. In previous papers, colleagues and I argued for the importance of plant underground storage organs (USOs) in hominid evolution (Laden and Wrangham in press?; Wrangham, et al. 1999). Roots and similar plant structures are more common in drier environments than in moist forests, so the spread of woodland, savanna, and arid lands would result in the rise of a “USO niche.” We show that such a niche likely emerged prior to the time of the adaptive radiation proposed here and expanded through the Pliocene and into the Pleistocene (Laden and Wrangham in press?). The argument has two major phases, one in which roots are incorporated as part of the diet of chimpanzee-like early hominids or the LCA of chimps and humans, and the second in which roots and other food products are processed with the novel adaptation of controlled fire (the origin of cooking), changing the overall availability of food and increasing total dietary energy available to hominids.

The first use of roots would have involved a shift (in an essentially frugivorous chimp-like LCA) from using terrestrial herbaceous vegetation (THV) as a fallback food, to using plant underground storage organs (USOs) as a fallback food. Ultimately, just as gorillas are today capable of subsisting for long period on their “fallback food” (THV), we suggested that some populations of australopithecines would have done so with USOs. In all cases, megadonty and associated adaptations of the masticatory system would facilitate USO use, partly because this food source is of low caloric quality, and partly because breaking down starches of this type is done in the mouth (with amylase enzymes in saliva) rather than in the stomach or intestines. In a sense, robust australopithecines were to Pliocene hominids what gorillas are to living hominoids, but instead of being large of body and gut (as are gorillas) they are simply large-headed, with giant molarized teeth with thick enamel, large mouths (high palettes) and possibly (we can only guess) very potent parotid glands for producing copious amounts of amylase rich saliva.

Digging for roots would have been possible with chimp-like technology, and indeed, there are chimps today in the Congo that dig up and use water from roots (Wrangham and Peterson 1996). Using sharpened sticks as many people do today to dig up roots would have been an important advance. Given that the early Oldowan tools that have been examined for use wear show extensive evidence of use in working wood, as well as the animal bones provisionally identified in South African deposits as modified from digging (Shipman 2001) it seems reasonable to suggest that early technologies were at least in part in support of this dietary regime.

Early australopithecines show adaptations that one would expect for an animal that incorporated roots as an important part of the diet. Later australopithecines (Phase II), especially paranthropines, show adaptations that one would expect if USOs had become of primary importance. The rise of possible paranthropine USO-specialists at the same time as the first clear use of stone tools may be more than just a coincidence. Some or all hominids could have been using digging sticks, shaped and sharpened with chipped stone tools.

The second major diet shift would have come somewhat later (Wrangham, et al. 1999) and involved cooking these USOs as well as other food products. Cooking would detoxify many otherwise inedible foods, in some cases enhanced the total caloric value of foods (some roots are so enhanced by cooking), and significantly decreased the difficulty of mastication. Starchy USO's would be in a sense pre-digested, and the total available dietary energy would be substantially increased, thus helping to explain and understand the reduction in tooth size and masticatory apparatus, and enormous increase in body size (a virtual doubling) that is observed with *Homo erectus/ergaster*.

Referring again to Figure 5, while it is likely that the major ca 2.6 mya event identified by Vrba as associated with bovid evolution was important both to bovids and to hominids, it is also clear that bovid evolution does not have the same exact pattern as hominid evolution. Both taxa experience increased speciation at just around this time, but previously, hominids seem to be diversifying at a greater rate than bovids, and later, bovids seem to experience another increase in speciation just as the hominid clade is being trimmed down by species loss. Although Figure 5 does not show bovid last appearances (for simplicity) it is notable that today, Africa has one species of hominid and dozens of species of bovids. Obviously, while both taxa were affected sometimes by large events, the two taxa show very different overall patterns of evolution. This

is important, because the connection between bovid evolution and hominid evolution implies at least two things that may not be true: A connection between hominid evolution and the spread of grasslands, implying adaptation to very open environments, and a connection between hominid evolution and bovid diversity, with bovids being part of the expanding prey for early hominid hunters. However, neither of these phenomena is really indicated in the fossil record.

And this should not be too much of a surprise. There is no reason why an ape taxon should closely follow bovid taxa in evolutionary history. The same major climatic events may affect both but there is every reason to expect the effect to be different for the different taxa. Furthermore, following the insight of Simpson mentioned earlier, it is likely that the nature of a particular adaptation may shift over time as the context of the adaptation shifts. Imagine, for example, that the objective is simply to acquire and consume roots. An animal with digging hands would have access to such a resource, but only certain quantities in certain environments. Adding a digging stick would add environments in which USOs could be harvested by including a wider range of geological conditions, but would not change access to roots based on varying toxicity. Adding cooking of roots to the adaptive “toolkit” would then change the range of species of USO that could be safely consumed. As each of these transitions occurred, the physical habitat in which the hominid could live would change, and along with that would also change the range and nature of competitors, predators, and other resources available to that hominid.

Such a sequence of events helps also to explain the general, but not detailed, correlation between hominid and bovid evolutionary patterns. The newly evolving bovids of the Pliocene were mainly eating grasses, though some were certainly browsers. Hominids are unlikely to have ever eaten grass, and many kinds of leaves browsed by these bovids would also have been inaccessible (compared to the forest THV of living forest apes). Since bovids and hominids would have had entirely different diets, there is no reason that their macroevolutionary patterns would be very similar. Both taxa responded to a trend in climate-caused habitat change, but in different ways, because they were responding to different parts of the newly emerging and expanding habitats.

Discussion

In 1999, Robert Foley tested the hominid palaeontological record for evidence of an “association of hominid evolution [and] a period of global climatic instability and cooling” as a

prelude to understanding a possible causal relationship between the two. This work was inspired by earlier work by others who suggested and provided evidence for such an association (Bromage and Schrenk 1995a; Grine 1988; Vrba 1989; Vrba 1996b; Vrba 1999). Foley concluded that “Climate does have an effect on hominid and other primate evolution, but this is not directly related to speciation or the appearance of new taxa.”(Foley 1994). Foley found a better correlation between climate change and extinction. However, Foley had made an effort to link climate events in short (500 kyr and 100 kyr) time periods to changes in the fossil record, and two factors conspired against the success of that test: 1) The inadequacy of the record, and 2) the fact, as proposed here, that this adaptive radiation was a phenomenon that occurred on a larger temporal scale than the one at which Foley was working.

McHenry (McHenry 1994) and Stanley (Stanley 1992), in explicit efforts to examine the hominid fossil record from a macroevolutionary perspective, both concluded that the “pattern of morphological change in the hominid lineage was mosaic”(McHenry 1994). Both identified parallel evolution in cranio-dental and/or brain size changes, a phenomenon which has been examined by others (Bromage and Schrenk 1999; Grine 1988; Pilbeam and Gould 1974; Turner and Wood 1993). The work presented here does not contradict Stanley and McHenry’s assertions, but places them in a different framework. The idea of “mosaic” implies a final product stitched together in pieces. However, at 4.0 million years ago, there existed one or more (but not a great number of) species of australopithecines with modest megadonty, some kind of bipedalism, and an otherwise essentially chimp-like morphology, behavior, and habitat preference. Their tendency to acquire and consume USOs as well as the more traditional gorilla fallback food of THV would have made human observers take special note. Nonetheless, Phase I australopiths were a final product in and of themselves, and their “preadaptations” are “pre” anything only in retrospect. Phase II hominid adaptations included a mixture of those things typically associated with australopithecines, such as megadonty, and those things associated with *homo*, distributed unevenly among a range of species. The most divergent of hominids existed during this period, quite possibly with many different combinations of australopithecine-like vs. “modern” postcranial forms, different degrees of megadonty and associated masticatory adaptations, different degrees of brain size, and we may speculate, different degrees of stone tool use and possibly even use of fire. All of these different Phase II hominids were in competition with each other and other species, at the macroevolutionary level, in the invasion of newly

opening niches in drier, more open, seasonal habitats. Plant USOs were rare but potentially important prior to about 3 million years ago, but the relatively obscure chimpanzee-like early hominids were at least partly adapted to make use of them. When USO rich niches became “the thing” in the Pliocene, many taxa took advantage. This is when we see the expansion of hominids, but also of suids, and possibly ursids (Hatley and Kappelman 1980). In the meantime, grasslands were also expanding, significantly but not perfectly overlapping in time and space with USO-rich habitats (the latter also being common in more arid and somewhat wetter areas with less grass).

It would not be surprising to find that an earlier hominid radiation had occurred, perhaps in Central Africa in what is now the northern rim of the Sahel and the southern arid regions of North Africa. It would be surprising to find early (Late Miocene) hominids represented abundantly in southern or even eastern Africa. It would also be surprising if the general shape of the Phase II adaptive radiation were to change very much with additional work. Although tentative, these assertions can be made because the intensive and extensive work by several researchers in this period, and this region, has been very successful in generating an excellent fossil record. Nonetheless, sample sizes for many time periods are too small, taxonomic issues are still very much at large, and major biological questions remain, such as the degree of sexual dimorphism in any given taxon, and more precise understanding of each taxon’s biogeography and habitat preference.

Table 1. Two alternative lists of hominid species: 1a maximizes species diversity by including more species than may be generally recognized, with the expectation that some of the less well established species represent, minimally, real variation in the fossil record; 1b reduces species diversity and disparity by sinking very similar forms into inclusive categories that do not include excessive variation. Sources for these lists include several summary papers or anthology chapters and the references therein, most notably (Brain 1988; Bromage and Schrenk 1999; Bromage, et al. 1995; Brown, et al. 2001; Brunet, et al. 1995; Brunet, et al. 2002; Clarke 1998; Clarke 1999; Clarke and Tobias 1995; Coffing, et al. 1994; Day, et al.; Foley 2002; Foley 1994; Gibbons 2003; Grine and Daegling 1993; Grine and Strait 1994; Harris, et al. 1994; Kappelman, et al. 1996; Keyser 2000; Leakey and Harris J.M. 1987; Leakey and Hay 1983; Leakey, et al. 1995; Leakey, et al. 1998; Leakey, et al. 2001a; Leakey and Isaac 1976; Leakey and Walker 1985; McKee 1993; Partridge, et al. 2003; Plummer and Potts 1995; Schwarcz, et al. 1994; Senut, et al. 2001; Thackeray, et al. 2003; Turner, et al. 1999; Vignaud, et al. 2002; Vrba 1995a; Vrba 1995b; Walker 2002; Ward, et al. 1999; White 1995; White, et al. 2000; White 1994; Wood 1996a; Wood 1996b).

Table 1a. Spliiter's list of hominds

Hominid	First appearance	Last appearance	Midpoint
Sahelanthropus tchadensis	7	6	6.5
Ardipithecus ramidus	5.5	4.3	4.9
Australopithecus anamensis	4.18	3.95	4.065
Australopithecus afarensis	3.8	2.3	3.05
Australopithecus sp	3.58	3.2	3.39
Australopithecus bahrelghazali	3.5	3	3.25
Australopithecus africanus	3.4	2.3	2.85
Kenyanthropus platyops	3	2.7	2.85
Australopithecus crassidens	2.8	2.3	2.55
Paranthropus aethiopicus	2.52	1.86	2.19
Homo habilis	2.42	1	1.71
Homo sp	2.33	0.6	1.465
Paranthropus boisei	2.3	1	1.65
Homo rudolfensis	2.2	1.88	2.04
Paranthropus robustus	2	1	1.5
Homo ergaster	1.88	1	1.44
Homo sapiens	0.6	0.127	0.3635

Table 1b: Lumped and adjusted list of hominids

Hominid	First appearance	Last appearance	Midpoint
Sahelanthropus tchadensis	7	6	6.5
Early East African Gracile Au	5.5	2.3	
Australopithecus africanus	3.4	2.3	2.85
Kenyanthropus platyops	3	2.7	2.85
Australopithecus crassidens	2.8	2.3	2.55
Paranthropus aethiopicus	2.52	1.86	2.19
Homo habilis	2.42	1	1.71
Homo sp	2.33	0.6	1.465
Paranthropus boisei	2.3	1	1.65
Homo rudolfensis	2.2	1.88	2.04
Paranthropus robustus	2	1	1.5
Extended Homo ergaster/erec	1.88	0.04	0.96
Extended H. sapiens, gracile	0.1	0	0.05



Figure 1. Phylogeny-free rank ordered diagram (ordered by date of first appearance) of hominids based on Table 1b. The shaded area represents the time during which there was a concentration of first appearances suggesting a species radiation. The shaded area is drawn slightly older than the earliest fossil within it to account for current controversy over the age of the South African hominids.

Figure 1

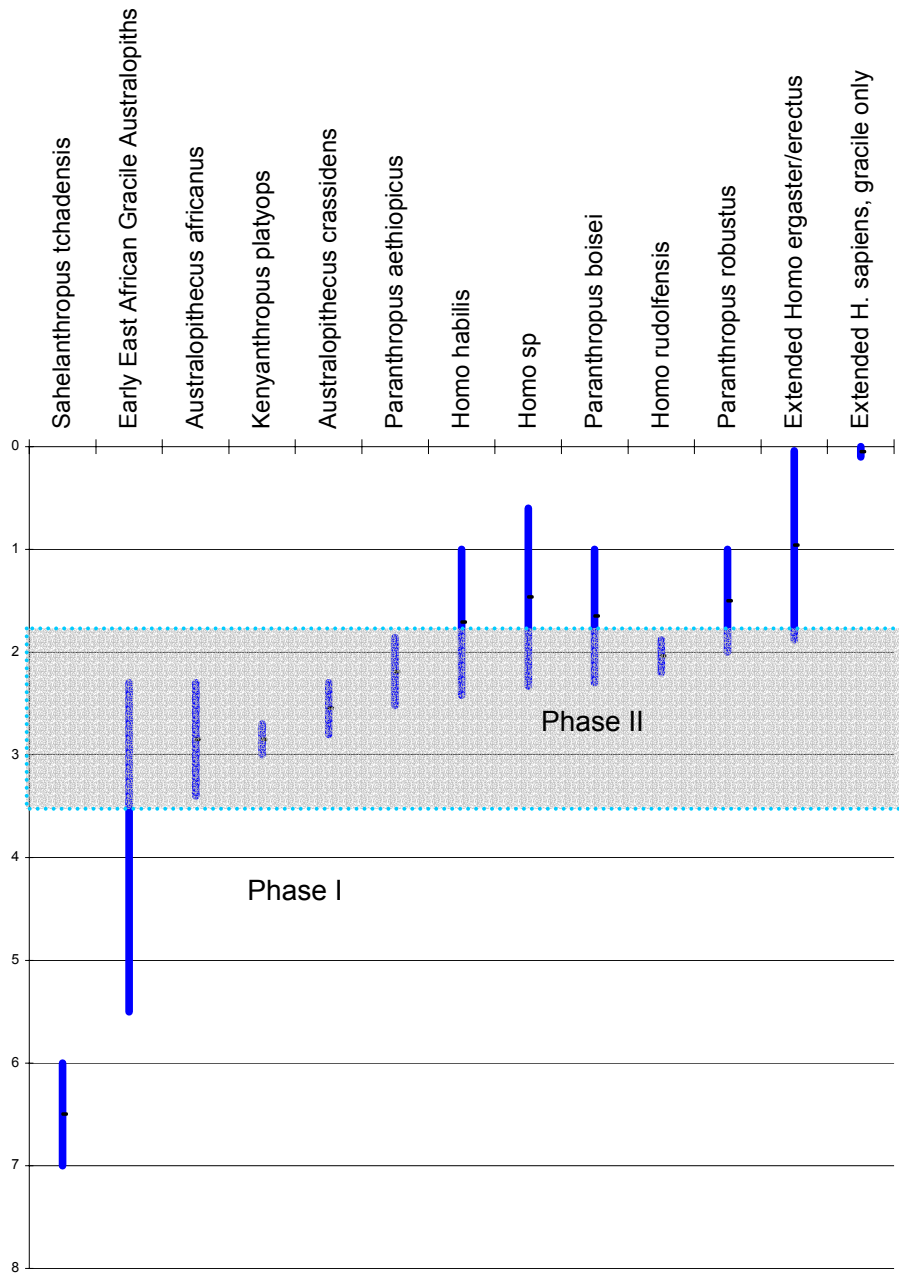


Figure 2. Each line represents a ranked-order series of dates representing either hominid species, finds spots of hominids, or find spots of mammalian fossils whether or not hominids were found on that find spot. The longest, pink line on the right shows the distribution of specific mammalian fossil find localities throughout Africa, regardless of whether hominids are present, culled from numerous sources as outlined in Appendix 1. Relatively vertical sections of this line indicate relatively poorer representation of the fossil record. Clearly, the fossil record is of roughly equal quality from somewhere around 4.5 mya until 1.0 mya. The dark blue line (second longest line to the left) is the same data set but only including hominid find spots. This shows that the hominid record is of high quality after 4.0 mya, but more importantly, that prior to 4.0 mya, the African mammalian fossil record is of fairly good quality, suggesting that if hominids were as common prior to 4.0 mya as they are after 3.0 mya, there should be more evidence from them. The brown line is the distribution of the hominid species (midpoint dates) from Table 1b. The light blue line to the far left is the distribution of hominid species known much earlier from a earlier sources (McHenry 1994; Stanley 1979). The contrast between these two hominid lines is dramatic, and shows that we now know at least two things we did not know before: 1) the hominid fossil record may be “clumped” (in terms of species diversity) during this period of species radiation, and 2) the hominid record may is older than would have been initially inferred just from the fossil record (absent DNA divergence estimates) in the 1970s and through the early 1980s.

Figure 2.

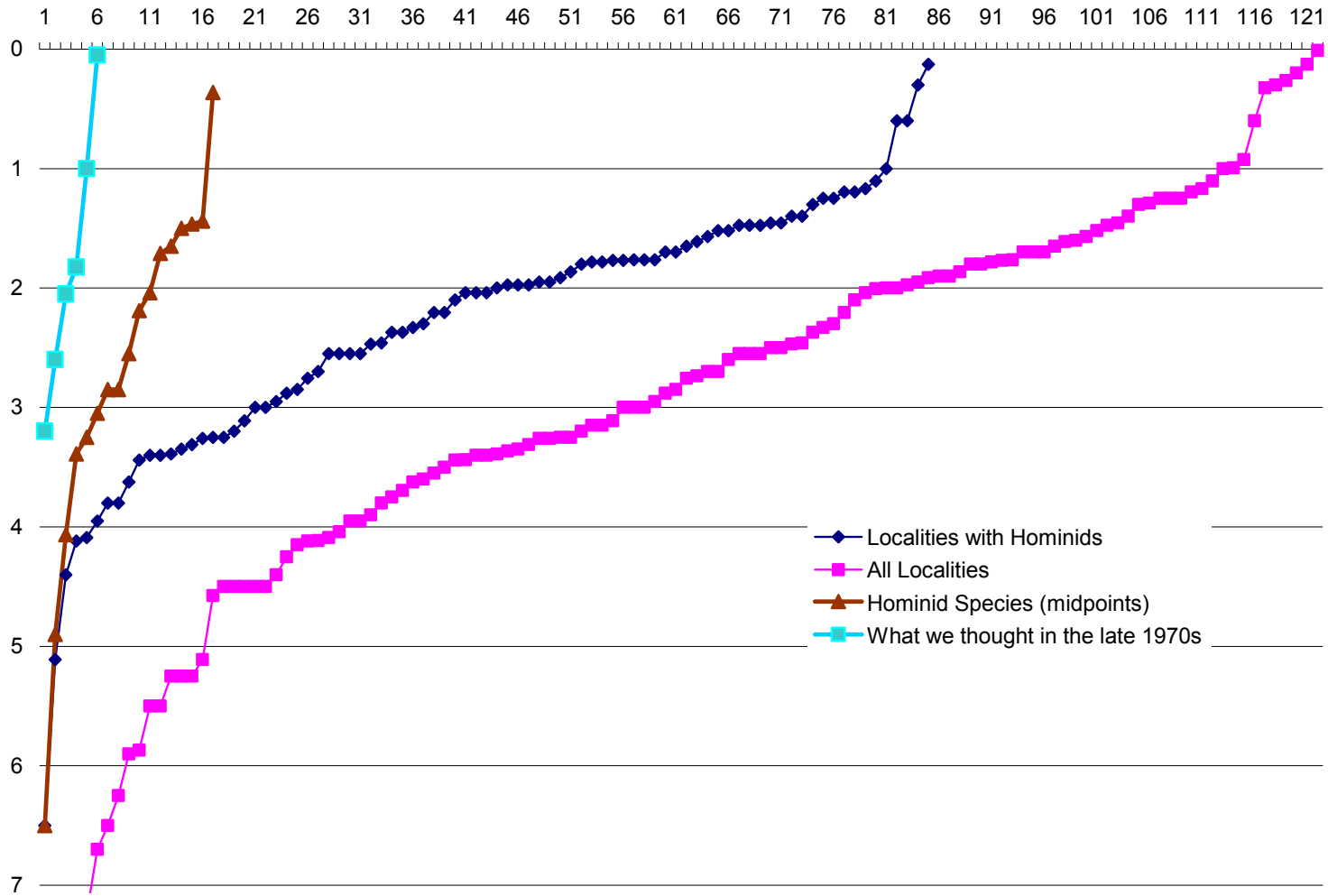


Figure 3. The “Evolution” of the hominid fossil record is depicted schematically here from left to right. For each of the five different (A – E) depictions are given the estimated age range for each taxon, and a line (green dashed) showing the pattern of diversity over time. The green pattern line would be un-kinked or straight for an uninteresting, phyletic, gradual fossil record, and relatively kinked for a fossil sequence that contains an adaptive radiation. A: Early conceptualization of the fossil record as it stood in the 1970s and early 1980s, drawn from the same source as for Figure 2; B: A somewhat updated series showing species generally considered prior to the discovery of *A. ramidus*; C: A version of hominid evolution adapted from the informative yet fantastical diagram of Wood and Brooks (1999) in which they attempt to show in a summary article that diversity is starting to reign in the early hominid record by including many unnamed species in time/space/adaptive zones not yet filled by actual fossil finds; D: The diversity-maximizing hominid list from Table 1a; and E: The diversity reducing list from Table 1b. The most important take home message from this “evolutionary” depiction of conceptions of hominid evolution is that we have shifted from a tendency to extend diversity from the better known time periods into the past, which is in contrast to the most plausible view based on available data, suggested in this paper, that there is a real change in the level of diversity from Phase I to Phase II periods of hominid evolution.

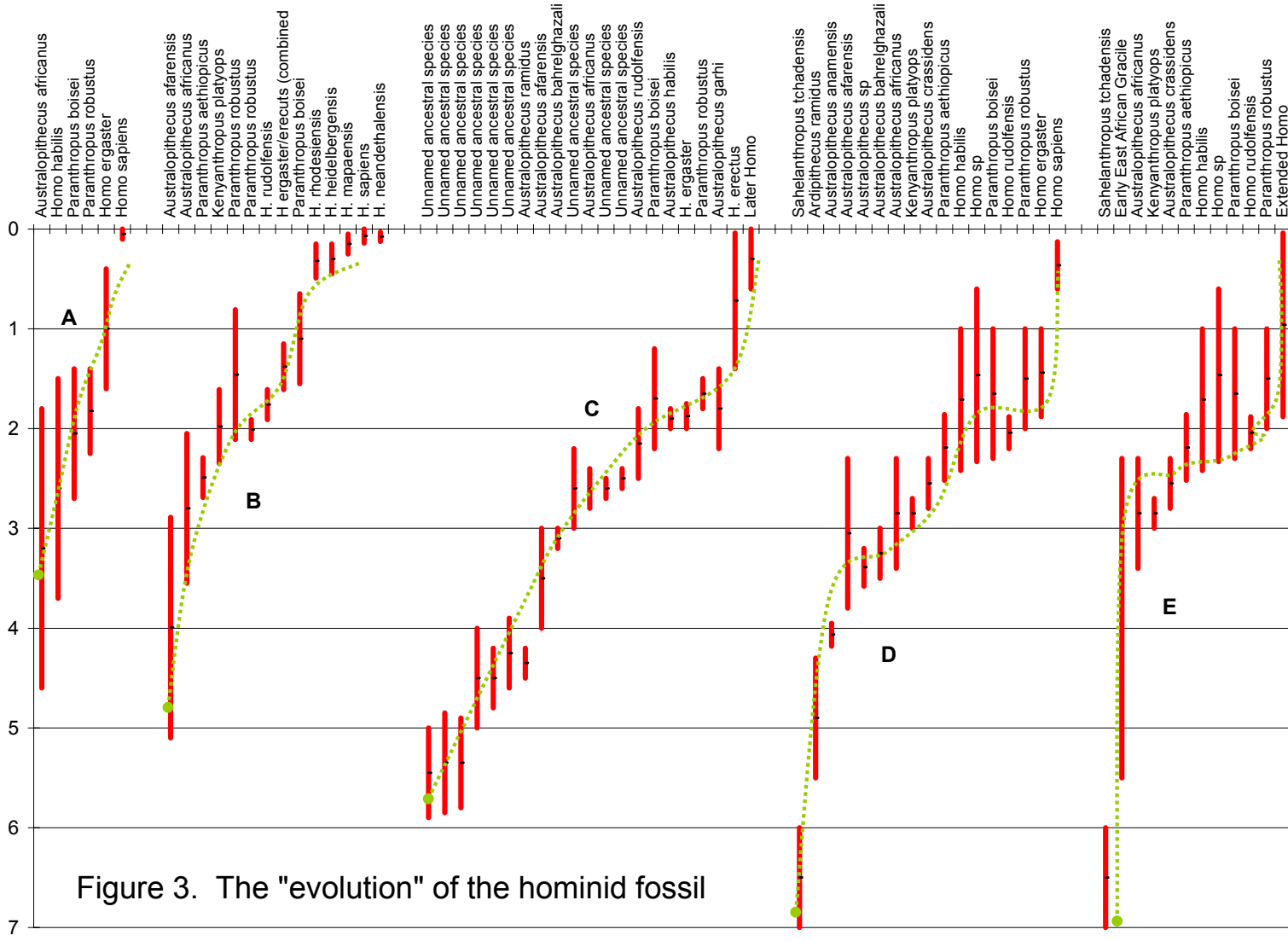
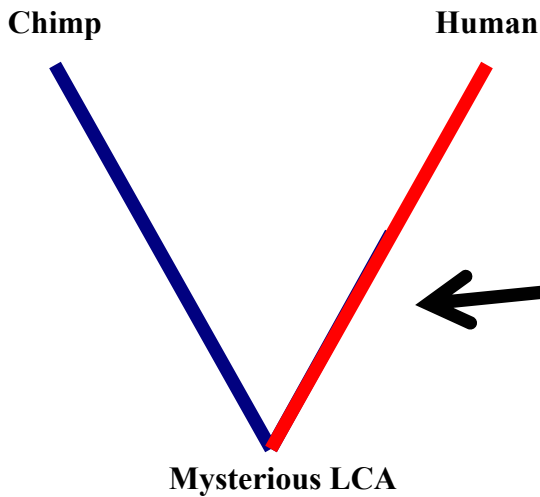


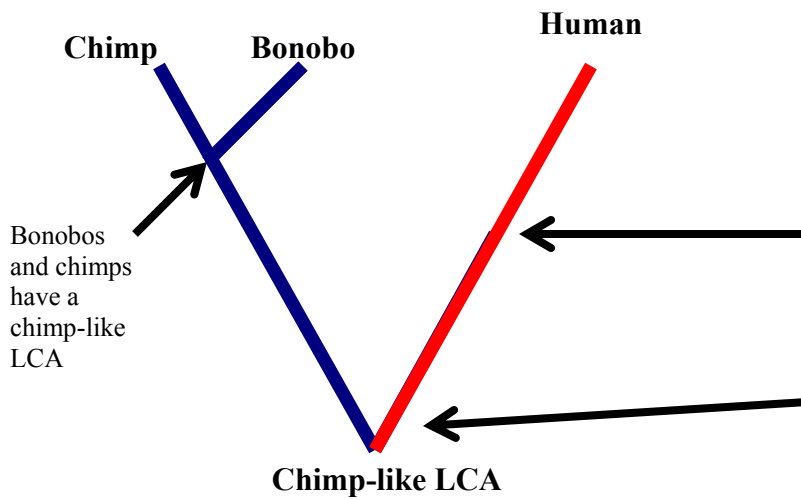
Figure 3. The "evolution" of the hominid fossil

Figure 4. This diagram is meant to re-orient thinking about hominid evolution to recognize the “chimpness” of the first half (or so) of the fossil record including Phase I as defined in this paper, as distinct from the “australopithiceness” of the period of the Phase II radiation.

Figure 4.



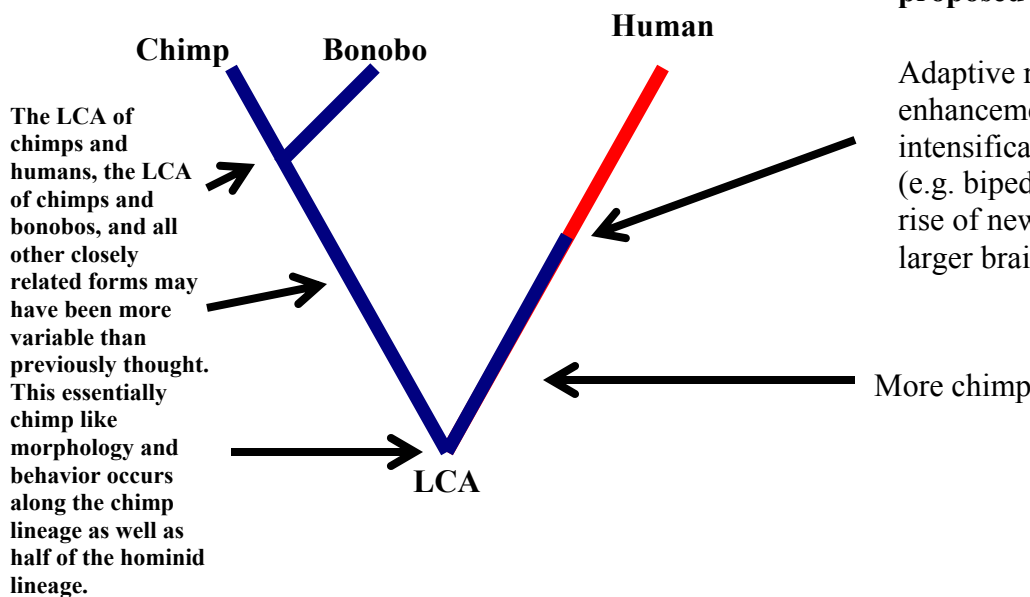
Earliest conceptions of hominid evolution: Co-evolving unique human traits, including bipedalism/upright posture, freeing of the hands, technology, brain enlargement, etc.



More recent conceptions of hominid evolution:

Increased brain size, more advanced technology, origin of genus *Homo*.

Origin of bipedalism, megadonty, changes in diet and habitat, "Leaving the trees," origin of *Australopithecus* and related species



Conception of hominid evolution proposed here:

Adaptive radiation including enhancement, modification, and intensification of pre-existing traits (e.g. bipedalism and megadonty) and rise of new traits (lithic technology, larger brain).

Figure 5. Correlated and contrasting views and data sets related to hominid evolution (see text).

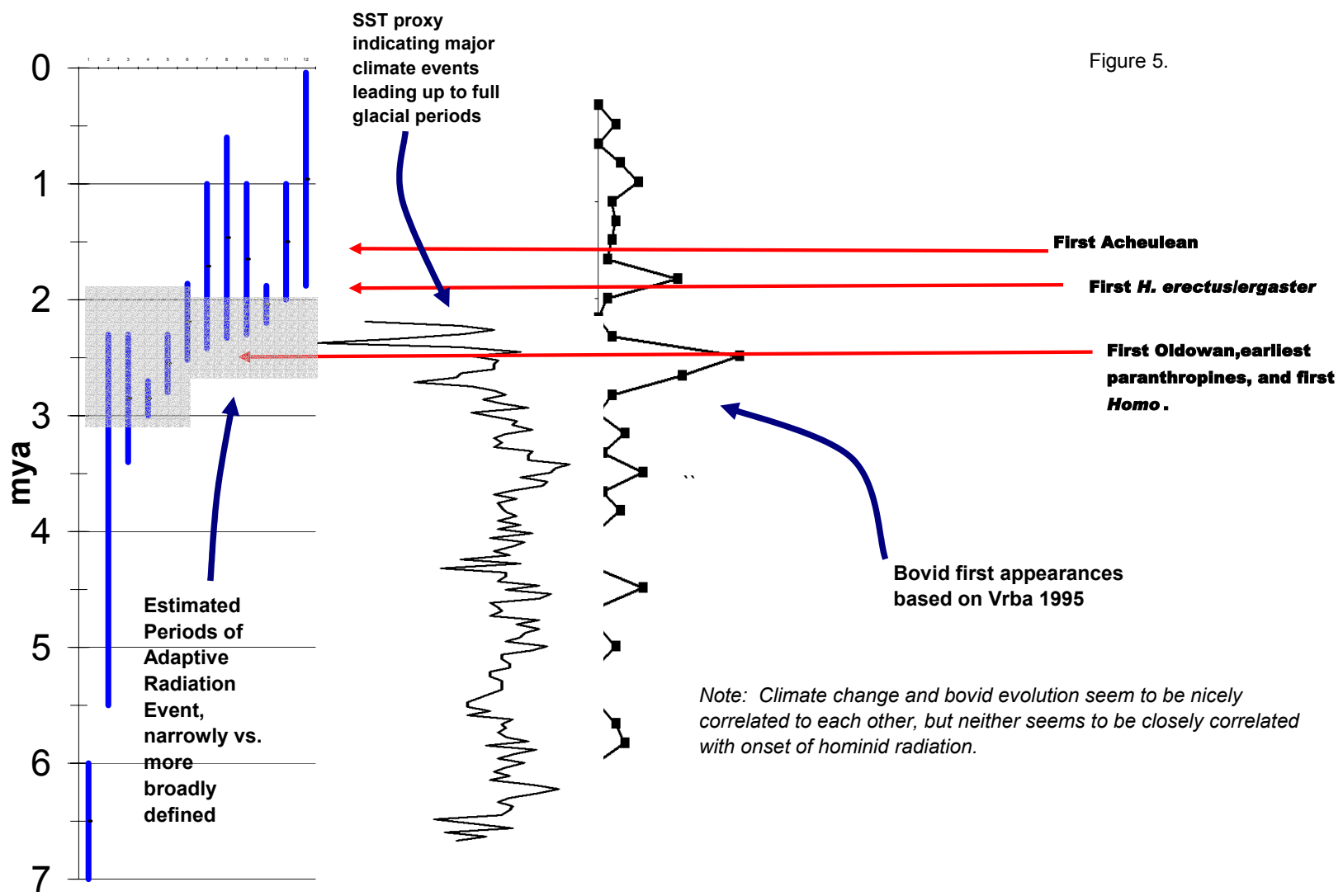


Figure 5.

Note: Climate change and bovid evolution seem to be nicely correlated to each other, but neither seems to be closely correlated with onset of hominid radiation.

- Boaz NT, Dechamps R, Delson E, Gentry AW, Harris JWK, Meylan P, Pavlakis PP, Sanders WJ, Stewart KM, Verniers J and others. 1992. New evaluation of the significance of the Late Neogene Lusso Beds, upper Semliki Valley, Zaire. *Journal of Human Evolution* 22(6):505-517.
- Brain CK. 1988. New information from the Swartkrans Cave of relevance to "robust" australopithecines. *Evolutionary History of the "Robust" Australopithecines*: New York : Aldine de Gruyter.
- Brain CK. 1995. Influence of climatic changes on the completeness of the early hominid record in Southern African caves, with particular reference to Swartkrans. *Paleoclimate and Evolution, with Emphasis on Human Origins*: New Haven : Yale University Press.
- Bromage TG, Schrenk F. 1995a. Biogeographic and climatic basis for a narrative of early hominid evolution. *Journal of Human Evolution* v. 28, no. 1, 1995. pp. 109-114.
- Bromage TG, Schrenk F. 1995b. Biogeographic and climatic basis for a narrative of early hominid evolution. *Journal of Human Evolution* 28(1):109-114.
- Bromage TG, Schrenk F. 1999. *African biogeography, climate change & human evolution*. New York: Oxford University Press. ix, 485 p.
- Bromage TG, Schrenk F, Zonneveld FW. 1995. Paleoanthropology of the Malawi Rift: An early hominid mandible from the Chiwondo Beds, northern Malawi. *Journal of Human Evolution* 28(1):71-108.
- Brown B, Brown FH, Walker A. 2001. New hominids from the Lake Turkana Basin, Kenya. *Journal of Human Evolution* 41:29-44.
- Brunet, Beauvilain C, Heintz, Moutaye, Pilbeam. 1995. The first australopithecine 2,500 kilometers west of the Rift Valley (Chad).
- Brunet M, Guy F, Pilbeam D, Mackaye HT, Likius A, Ahounta D, Beauvilains A, Blondel C, Bocherens H, Boisserie J-R and others. 2002. A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* 418:145-151.
- Clarke RJ. 1998. First ever discovery of a well-preserved skull and associated skeleton of *Australopithecus*. *South African Journal of Science* 94(10):460-464.
- Clarke RJ. 1999. Discovery of complete arm and hand of the 3.3 million-year-old *Australopithecus* skeleton from Sterkfontein. *South African Journal of Science* 95:477-480.
- Clarke RJ, Tobias PV. 1995. Sterkfontein Member 2 foot bones of the oldest South African hominid. *Science* 269(5223):521-524.
- Coffing K, Leakey M, Walker A, Feibel C. 1994. Four-million-year-old hominids from East Lake Turkana, Kenya. *American Journal of Physical Anthropology* 93(1):55-65.
- Collard M, Wood B. 2001. Homoplasy and the early hominid masticatory system: inferences from analyses of extant hominoids and papionins. *Journal of Human Evolution* 41(3):167-194.
- Dart RA. 1925. The African manlike ape skull. *Scientific monthly* 20:334-336.
- Darwin C. 1874. *The Descent of Man*. New York: A. L. Burt.
- Day H, Leakey M, Magori C. A new hominid fossil skull (:LH 18) from Ngaloba beds, laetoli, northern tanzania.
- Foley R. 2002. Adaptive radiations and dispersals in Hominin evolutionary ecology. *Evolutionary Anthropology Supl* 1:32-37.

- Foley RA. 1994. Speciation, extinction and climatic change in hominid evolution. *Journal of Human Evolution* v. 26, no. 4, 1994. pp. 275-289.
- Gibbons A. 2003. Great age suggested for South African hominids. *Science* 300:562.
- Grine FE. 1988. Evolutionary history of the "robust" australopithecines: a summary and historical perspective. *Evolutionary History of the "Robust" Australopithecines*:509-520.
- Grine FE, Daegling DJ. 1993. New mandible of *Paranthropus robustus* from Member 1, Swartkrans Formation, South Africa. *Journal of Human Evolution* 24(4):319-333.
- Grine FE, Strait DS. 1994. New hominid fossils from Member 1 "Hanging Remnant", Swartkrans Formation, South Africa. *Journal of Human Evolution* v. 26, no. 1, 1994. pp. 57-75.
- Harris J, Walker A, Leakey M. 1994. Note on the reported occurrence of very early *Homo* from West Lake Turkana, Kenya. *Journal of Human Evolution* 27(5):447-448.
- Harrison T, editor. 1997. Neogene paleontology of the Manonga Valley, Tanzania: A window into the evolutionary history of East Africa. New York and London: Plenum Press.
- Harrison T, Baker E. 1997. Paleontology and biochronology of fossil localities in the Manonga Valley, Tanzania. In: Harrison T, editor. Neogene paleontology of the Manonga Valley, Tanzania: A window into the evolutionary history of East Africa. New York and London: Plenum Press. p 361-392.
- Hatley T, Kappelman J. 1980. Bears, pigs, and plio-pleistocene hominids: a case for the exploitation of belowground food resources. *Human ecology* 8(4):371-387.
- Hawkes, O'Connell, Jones B. 1997. Hadza women's time allocation, offspring provisioning, and the evolution of long postmopausal life spans.
- Hill A. 1985. Early hominid from Baringo, Kenya. *Nature* 315:222-224.
- Kappelman J, Swisher CCI, Fleagle JG, Yirga S, Bown TM, Feseha M. 1996. Age of *Australopithecus afarensis* from Fejej, Ethiopia. *Journal of Human Evolution* v. 30, no. 2, 1996. pp. 139-146.
- Kay R. 1981. The nut-crackers: a new theory of adaptations of the ramapithecinae.
- Keyser AW. 2000. The Drimolen skull: the most complete australopithecine cranium and mandible to date. *South African Journal of Science* 96:189-193.
- Kimbel WH. 1995. Hominid speciation and Pliocene climatic change. *Paleoclimate and Evolution, with Emphasis on Human Origins*: New Haven : Yale University Press.
- Kingston JD, Jacobs BF, Hill A, Deino AL. 2002. Stratigraphy, age and environments of the late Miocene Mpesida Beds, Tugen Hills, Kenya. *Journal of Human Evolution* 42:95-116.
- Laden G, Wrangham R. in press? The Rise of the Hominids as an Adaptive Shift in Fallback Foods: Plant Underground Storage Organs (USOs) and the Origin of the Australopithecines. *Journal of Human Evolution*.
- Leakey M. 1999. Hominid Evolution: Introduction. *African biogeography, climate change & human evolution*. New York and Oxford: Oxford University Press. p 271-275.
- Leakey MD, Harris JM., editors. 1987. Laetoli, A Pliocene site in northern Tanzania. Oxford: Oxford University Press.
- Leakey MD, Hay RL. 1983. Exploration and research at Olduvai Gorge and Laetoli, Tanzania, 1974-1980. Research reports - National Geographic Society 15:379-386.
- Leakey MG, Feibel CS, McDougall I, Walker A. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376(6541):565-71.

- Leakey MG, Feibel CS, McDougall I, Ward C, Walker A. 1998. New specimens and confirmation of an early age for *Australopithecus anamensis*. *Nature* 393(6680):62-6.
- Leakey MG, Spoor F, Brown FH, Gathogo PN, Kiarie C, Leakey LN, McDougall I. 2001a. New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature* 410:433-440.
- Leakey MG, Spoor F, Leakey LN, Brown FH. New hominin discoveries from the Nachukui Formation, west of Lake Turkana; 2001b. *American Journal of Physical Anthropology*.
- Leakey REF, Isaac GL. 1976. East Rudolf: an introduction to the abundance of new evidence. *Perspectives on human evolution* 3, 1976:307-332: ill., graphs, plans.
- Leakey REF, Walker AC. 1985. Further hominids from the Plio-Pleistocene of Koobi Fora, Kenya. *American journal of physical anthropology* 67, no. 2, 1985:135-163, ill.
- Lieberman DE, Pilbeam DR, Wood BA. 1988. Probabilistic approach to the problem of sexual dimorphism in *Homo habilis*: a comparison of KNM-ER 1470 and KNM-ER 1813. *Journal of human evolution* 17, no. 5, 1988:503-511.
- Lieberman DE, Wood BA, Pilbeam DR. 1996. Homoplasmy and early *Homo*: an analysis of the evolutionary relationships of *H. habilis sensu stricto* and *H. rudolfensis*. *Journal of Human Evolution* v. 30, no. 2, 1996. pp. 97-120.
- Lovejoy CO. 1981. The origin of man.
- Lovejoy O. 1988. Evolution of human walking.
- McHenry HM. 1994. Tempo and mode in human evolution. *Proceedings of the National Academy of Sciences of the United States of America* 91(15):6780-6786.
- McKee JK. 1993. Faunal dating of the Taung hominid fossil deposit. *Journal of Human Evolution* 25(5, 1993):363-376.
- Partridge TC, Granger DE, Caffee MW, Clarke RJ. 2003. Lower Pliocene hominid remains from Sterkfontein. *Science* 300:607-612.
- Pickford M. 1991. What caused the first steps towards the evolution of walkie-talkie primates?
- Pilbeam DR, Gould SJ. 1974. Size and scaling in human evolution. *Science*.
- Plummer T, Potts R. 1995. Hominid fossil sample from Kanjera, Kenya: description, provenance, and implications of new and earlier discoveries. *American Journal of Physical Anthropology* v. 96, no. 1, 1995. pp. 7-23.
- Rightmire GP. 1995. Diversity within the Genus *Homo*. *Paleoclimate and Evolution, with Emphasis on Human Origins*: New Haven : Yale University Press.
- Roberts N. 1981. Pleistocene environments in time and space.
- Ruff CB. 1991. Climate and body shape in hominid evolution. *Journal of Human Evolution* v. 21, no. 2, 1991. pp. 81-105.
- Ruvolo M. 1997. Molecular phylogeny of the hominoids: inferences from multiple independent DNA sequence data sets. *Molecular Biology and Evolution* 14(3):248-265.
- Ruvolo M, Disotell T, Allard M, Brown W, Honeycutt R. 1991. Resolution of the African hominoid trichotomy by use of a mitochondrial gene sequence.
- Ruvolo M, Pilbeam D. 1986. Hominoid evolution: molecular and palaeontological patterns. Major topics in primate and human evolution. Bernard Wood, Lawrence Martin, and Peter Andrews, eds: Cambridge, Eng. : Cambridge University Press, 1986. p 157-160.
- Schluter D. 2000. The ecology of adaptive radiation. Oxford: Oxford University Press.
- Szwarcz HP, Grun R, Tobias PV. 1994. ESR dating studies of the australopithecine site of Sterkfontein, South Africa. *Journal of Human Evolution* 26(3):175-181.

- Semaw S. 2000. The world's oldest stone artefacts from Gona, Ethiopia: Their implications for understanding stone technology and patterns of human evolution between 2.6-1.5 million years ago. *Journal of archaeological science* 27:1197-1214.
- Senut B, Pickford M, Gommery D, Mein P, Cheboi K. 2001. First hominid from the Miocene (Lukeino Formation, Kenya). *C.R. Acad. Sci. Earth and Planetary Sciences* 332:137-144.
- Shipman P. 2001. What can you do with a bone fragment? *Proceedings of the National Academy of Sciences of the United States of America* 98(4):1335-1337.
- Singer R. 1961. The new fossil sites at Langebaanweg (South Africa). *Current Anthropology* 2(4):385-387. map.
- Stanley SM. 1979. *Macro-evolution pattern and process*. Baltimore and London: The Johns Hopkins University Press.
- Stanley SM. 1992. An ecological theory for the origin of Homo.
- Thackeray JF, McBride VA, Segonyane SP, Franklyn CB. 2003. Trace element analysis of breccia associated with the type specimen of *Australopithecus (Paranthropus) robustus* from Kromdraai. *Annals of the transvaal museum* 40:147-150.
- Turner A, Bishop LC, Denys C, McKee JK. 1999. Appendix: A locality-based listing of African Plio-Pleistocene Mammals. In: Bromage TG, Schrenk F, editors. *African biogeography, climate change, & human evolution*. New York, Oxford: Oxford University Press. p 369-399.
- Turner A, Wood B. 1993. Comparative palaeontological context for the evolution of the early hominid masticatory system. *Journal of Human Evolution* 24(4):301-318.
- Vignaud P, Dourine P, Mackaye HT, Likies A, Blondel C, Boisserie J-R, Bonis Ld, Eisenmann V, Etienne M-E, Geraads D and others. 2002. Geology and Palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. *Nature* 418:152-155.
- Vrba E. 1982. Biostratigraphy and chronology, based particularly on Bovidae, of southern hominid-associated assemblages: Makapansgat, Sterkfontein, Taung, Kromdraai, Swartkrans; also Elandsfontein (Saldanha), Broken Hill (now Kabwe) and Cave of Hearths. In: de Lumley MA, editor. *L'Homo erectus et la place de l'homme de Tautavel parmi les hominides fossiles*. p 707-752.
- Vrba E. 1988. The environmental context of the evolution of early hominids and their culture.
- Vrba E. 1988a. The environmental context of the evolution of early hominids and their culture.
- Vrba E. 1989. Late Pliocene climatic events and hominid evolution.
- Vrba ES. 1985. Ecological and adaptive changes associated with early hominid evolution. *Ancestors: the hard evidence*. Eric Delson, ed: New York : Alan R. Liss, 1985. p 63-71, ill.
- Vrba ES. 1988b. Late Pliocene climatic events and hominid evolution. *Evolutionary History of the "Robust" Australopithecines*: New York : Aldine de Gruyter.
- Vrba ES. 1995a. Fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. *Paleoclimate and Evolution, with Emphasis on Human Origins*: New Haven : Yale University Press.
- Vrba ES. 1995b. On the connections between paleoclimate and evolution. In: Vrba ES, editor. *Paleoclimate and Evolution, with Emphasis on Human Origins*: New Haven : Yale University Press. p 24-45.
- Vrba ES. 1996a. Climate, heterochrony, and human evolution. *Journal of Anthropological Research* v. 52, no. 1, 1996. pp. 1-28.

- Vrba ES. 1996b. Paleoclimate and evolution, with emphasis on human origins. New Haven, Ct.: Yale University Press. ix, 547 p.
- Vrba ES. 1999. Habitat theory in relation to the evolution in African Neogene biota and hominids. In: Bromage TG, Schrenk F, editors. African biogeography, climate change & human evolution. New York, Oxford: Oxford University Press. p 19-34.
- Walker A. 2002. New perspectives on the Hominids of the Turkana Basin, Kenya. *Evolutionary Anthropology* S1:38-41.
- Ward C, Leakey M, Walker A. 1999. The new hominid species *Australopithecus anamensis*. *Evolutionary Anthropology* 7(6):197-205.
- Ward CV, Leakey MG, Walker A. 2001. Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *J Hum Evol* 41(4):255-368.
- Ward S, Hill A. 1987. Pliocene hominid partial mandible from Tabarin, Baringo, Kenya. *American journal of physical anthropology* 72, no. 1, 1987:21-37, ill.
- White T, Johanson D, Kimbel B. 1981. *Australopithecus africanus*: its phyletic position reconsidered.
- White TD. 1983. "Hominoid clavicle" from Sahabi is actually a fragment of cetacean rib. *American journal of physical anthropology* 61, no. 2, 1983:239-244, ill.
- White TD. 1995. African omnivores: global climatic change and Plio-Pleistocene hominids and suids. *Paleoclimate and Evolution, with Emphasis on Human Origins*: New Haven : Yale University Press.
- White TD, Suwa G, Simpson S, Asfaw B. 2000. Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. *Am J Phys Anthropol* 111(1):45-68.
- White TD, Suwa, G., Asfaw B. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 371:306-312.
- Wood B. 1985. Early Homo in Kenya, and its systematic relationships.
- Wood B. 1992. Origin and evolution of the genus Homo. *Nature* 355(6363):783-790.
- Wood B. 1996a. Hominid palaeobiology: have studies of comparative development come of age? *American Journal of Physical Anthropology* 99(1):9-15.
- Wood B. 1996b. Human evolution. *Bioessays* 18(12):945-54.
- Wood B, Brooks A. 1999. Human evolution. We are what we ate. *Nature* 400(6741):219-220.
- Wrangham R, Pilbeam D. 2001. African apes as time machines. In: Galdikas B, Briggs N, Sheeran L, Shapiro G, Goodall J, editors. All apes great and small. New York: Plenum Publishers. p 5-17.
- Wrangham RW, Jones JH, Laden G, Pilbeam D, Conklin-Brittain N. 1999. The raw and the stolen: cooking and the ecology of human origins. *Current Anthropology* 40(5, 1999):567-594.
- Wrangham RW, Peterson D. 1996. *Demonic males : apes and the origins of human violence*. Boston: Houghton Mifflin. 350 p.