

Chapter 10

Comparative Evolutionary Models and the “Australopith Radiations”

Robert A. Foley

Abstract This paper makes a case for the more formal use of evolutionary models in trying to understand human evolution. As the fossil record for hominin evolution has accumulated, and the level of diversity recognized has increased, we have moved to viewing the evolutionary history of the lineage as a series of adaptive radiations, rather than as a process of continuous, within lineage, change. The australopithecines would be seen to represent one such radiation, diversifying phylogenetically and expanding geographically. It is assumed that this is a response to a combination of the evolution of bipedalism and the expansion of more open habitats. Such interpretations have been largely inductive, and little attention has been paid to the way in which processes such as adaptive radiations and dispersals have been analyzed more widely in evolutionary biology. In this paper the australopithecine radiation is examined in the context of a number of models that have been developed to identify adaptive radiations. The results suggest that while there is some evidence for adaptational directionality to the group, in other ways australopithecine evolution falls short of the criteria for an adaptive radiation. As an alternative, australopithecine diversity is looked at in the context of dispersal models and the distribution in Africa. Finally, as it is clear that such model-based approaches are very sensitive to scale, the pattern of early hominin evolution is compared to two events at different scales—the evolution of modern humans, and the diversity of the chimpanzee clade.

Keywords Anagenesis • Australopithecine diversity • *Australopithecus* • Cladogenesis • Dispersal models • Evolutionary theory • Geographical models

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Introduction

Paleoanthropology is a strongly empirical discipline. To some extent this is an inevitable consequence of being a field largely dependent upon the chance events of the history of discovery. If evolution is a tinkerer, as Jacob (1977) has called it, then palaeontology is the tinkerer’s apprentice—looking at the new parts of the fossil record as they come in, and trying to work out where they can be strapped on to the existing structure.

Although there are some exceptions (Vrba 1985; Foley 1987, 1991; Stanley 1992; Conroy 2002; Hunt 2003), the empirical evidence for human evolution has seldom been put up against formal models derived from evolutionary theory. Many might say that it would be a worthless exercise, as the history is what it is, and the history of any lineage, especially one as peculiar as our own, will simply reflect itself. This may be the case, and the pattern of human evolution may not fit any particular model, but there are a number of responses to this critique that are possible. One is that differences between the expectations of a model and what is observed are as informative as a good fit, for they make us ask questions about why the conditions of evolution should be different. Another is that models can help us to see where the gaps in our knowledge lie, or what might be critical data, and so direct future research. Most important, though, is that if we are to do more than describe the pattern of our evolutionary history, we need to have a means of accessing the processes involved.

There are two problems with exploring the australopithecine radiations—one is the word radiation, and one the word australopithecine. “Radiation” can be used casually, but it can also be a formal event—thus when is a radiation a radiation? To put this another way, what sort of evolutionary event, or events, comprise the evolution of the australopithecines. This question can be explored theoretically by placing the australopithecines into a comparative

framework—or expectations—and try to determine which one of these may best fit what we observe. The two primary contexts are firstly, the concept of adaptive radiation, and secondly, the evolutionary process of dispersal. As will emerge, the applicability of any model is highly influenced by scale, and I shall examine this by focusing on two more empirical frameworks—recent human evolution and chimpanzee genetic diversity. However, it is first necessary to consider how best to define the term australopithecine.

The Australopiths

“*Australopithecus*” is a problem because there is no clear consensus as to what should be included in this group. Broadly speaking there are three defensible positions on this:

1. *Australopithecus* comprises all the non-*Homo* materials and is simply the early parts of hominin evolution, characterised largely by the absence of the features that define *Homo*, and the presence of those that distinguish it from the African apes.
2. *Australopithecus* comprises all the non-*Homo* material, excluding those earliest hominins that lack indisputable evidence for bipedalism (*Sahelanthropus*, *Orrorin*, *Ardipithecus*)—i.e., this would be what was historically referred to as the “robust” and “gracile” australopithecines.
3. *Australopithecus* is a narrow genus, differentiated from *Homo*, *Paranthropus*, *Kenyanthropus* and the earliest hominins (*Sahelanthropus*, *Ardipithecus*, and *Orrorin*) by a set of apomorphies largely related to the shape of the cranium and dental characteristics. This may or may not, according to various authors (Wood and Collard 1999), include *Australopithecus habilis* and *Australopithecus rudolfensis*, normally placed into *Homo*. A more extreme view would be that *Australopithecus* refers solely to the type species, *Australopithecus africanus*, and *Australopithecus afarensis* is placed in *Praeanthropus africanus* (Strait and Grine 2004).

Each position has some support, and deciding between them is a question of how clearly monophyly can be established and taxonomic preference within that. On the one hand, it could be argued that a small lineage such as the hominins, in a broader comparative perspective, cannot really consist of seven genera, and therefore lumping all the smaller brained hominins into a single genus is, from a primatological perspective, the best solution. On the other hand, the earliest hominins are extremely poorly known, very diverse, and lack many of the traits that have traditionally been associated with *Australopithecus* (White et al. 2009,

and related papers). Of these, perhaps the most significant is a greater degree of bipedal adaptation than that found in extant apes, yet associated with no marked cranial expansion. In between, it can be argued that the dental specialisations of the robust australopithecines are sufficiently distinct to justify a generic separation on the basis of adaptive difference.

Here the *Australopithecus* radiation is used as a working hypothesis for a monophyletic lineage comprising *Australopithecus anamensis*, *A. afarensis*, *Australopithecus bahrelghazali*, *A. africanus*, and *A. garhi*, i.e., the less extreme version of option 3 above. To this group one would also add the recently described *A. sediba* (Berger et al. 2010; de Ruiter et al. 2013). The justification for this is that, from an evolutionary ecological perspective, this scale of evolutionary event may be amenable to analysis in ways that would be lost if a broader definition were adopted (i.e., sliding together multiple events and trends). The aim here is not to define either the lineage or its place in hominin evolution more broadly, but to place it into the context of evolutionary models and processes. According to Strait and Grine’s (2004) cladistic analysis, this group would be monophyletic, although technically it should also include a stem clade that would later give rise to *Paranthropus* or robust *Australopithecus* and possibly early *Homo*. Where necessary for the purposes of analysis these stem lineages are used as such.

Figure 10.1 shows the chronological and geographical distribution in the fossil record. Although there are uncertainties and variable resolutions for all of these, the most controversial part of this is, ironically, the type australopith, *A. africanus*. Not only are the dates of this still debated, ranging from a FAD of 4.0+ Ma (Partridge et al. 2003) to considerably less than 3.0 or even 2.0 Ma (Berger et al. 2002), but it is also far from clear whether or not there is more than one taxon represented in Sterkfontein (Grine 2013; Clarke 2013). A relatively conservative approach is adopted to this problem.

Anagenesis and Cladogenesis

It is implicit in this paper that *Australopithecus* evolution involves diversification. This is not, however, a universally held view. White (2003) has consistently been a proponent of minimal taxonomic diversity among hominins, and Kimbel et al. (2006) have proposed such a pattern for *A. anamensis* and *A. afarensis*. However, most recent researchers have tended to accept at least some level of diversity (Fleagle 1999), with either full cladogenesis or some level of geographically-based diversity (Foley 1999; Strait and Wood 1999; see Strait 2013) (Fig. 10.2).

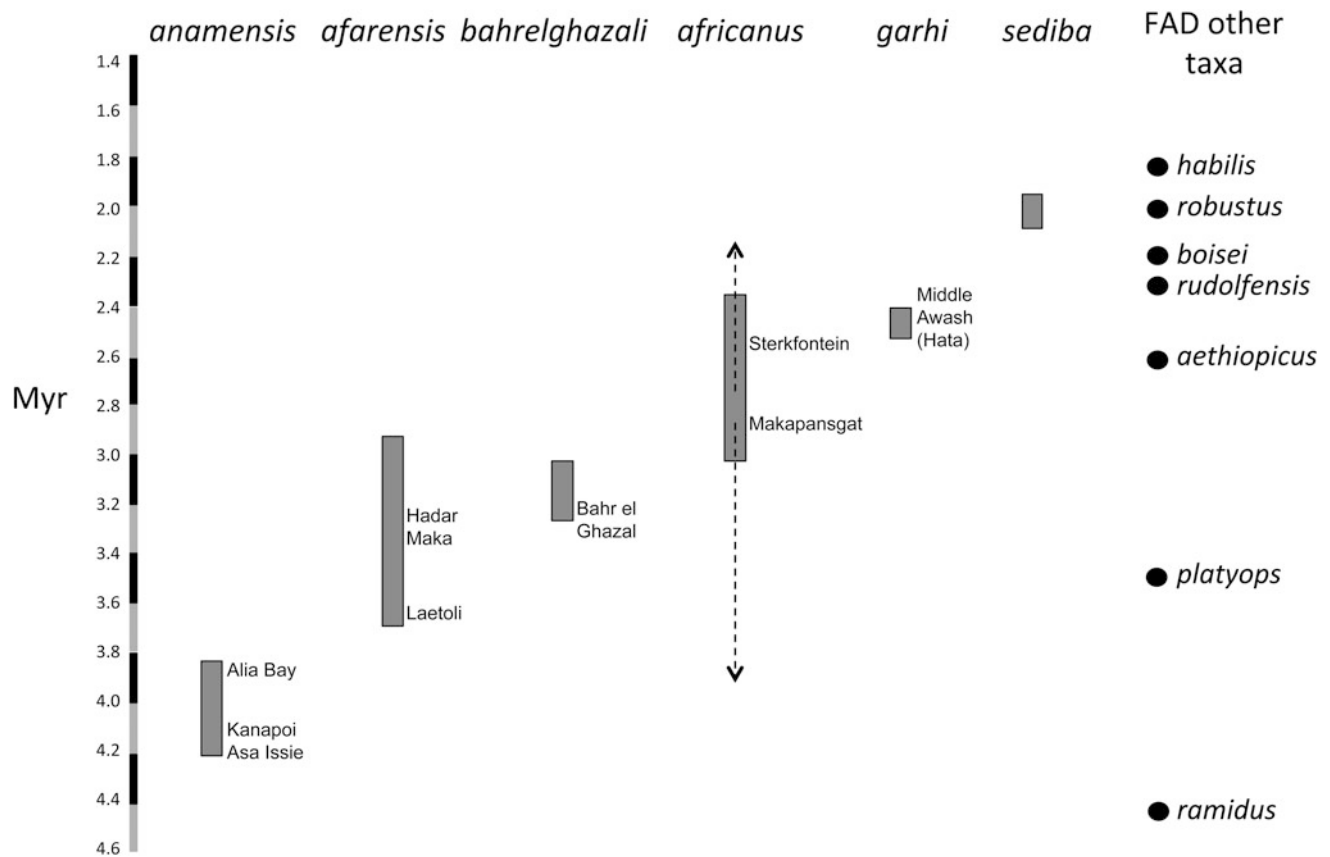


Fig. 10.1 Chronological distribution of the australopith taxa; the column on the right shows the first appearance points (FAD) of other hominin taxa that overlap chronologically. Scale in millions of years

To some extent differences between cladogenesis and anagenesis is a matter of process and scale. While anagenesis may be a fair description of a pattern seen from afar, it does not reflect an evolutionary process (Eldredge and Cracraft 1980). When we refer to species A evolving into species B, at a micro level this will be still be a process of cladogenesis. When a new species evolves, it will do so by the greater survivorship of some of its populations, relative to others. As this happens there will be declining reticulation among these populations, and it is this declining reticulation that comprises speciation. As can be seen from Fig. 10.3, there are three possible outcomes. However, in each case, some form of cladogenesis will have taken place; either the evolution of the daughter species and the extinction of the ancestral phenotype; or the evolution of the daughter species and the survival of the ancestral form (as a relict species, perhaps), or, perhaps, the evolution of two daughter species, and the extinction of the ancestral one. Although there are variable evolutionary outcomes, nonetheless, they are all forms of cladogenesis, with branching (declining reticulation) at the sub-specific level, leading to two species (one of which may become extinct).

For this reason, although we may observe a situation where at one time there is species A, and subsequently species B, nonetheless this is the result of cladogenesis, with one lineage becoming extinct. Although this may seem like splitting hairs, and that *A. anamensis* really does evolve into *A. afarensis*, it is important to understand the process by which it operates. One important implication of this is that it is perfectly possible for *A. anamensis* to “evolve into” *A. afarensis*, and yet still to exist. In the same vein, the co-existence of *H. erectus* and *H. habilis* does not necessarily prevent the latter being the ancestor of the former (Spoor et al. 2007).

Is There an Australopith Radiation?

The description of hominin evolution as a series of radiations has become relatively common in recent years (Foley 2002). However, exactly what is meant by an adaptive radiation, and how does one assess whether one has occurred?

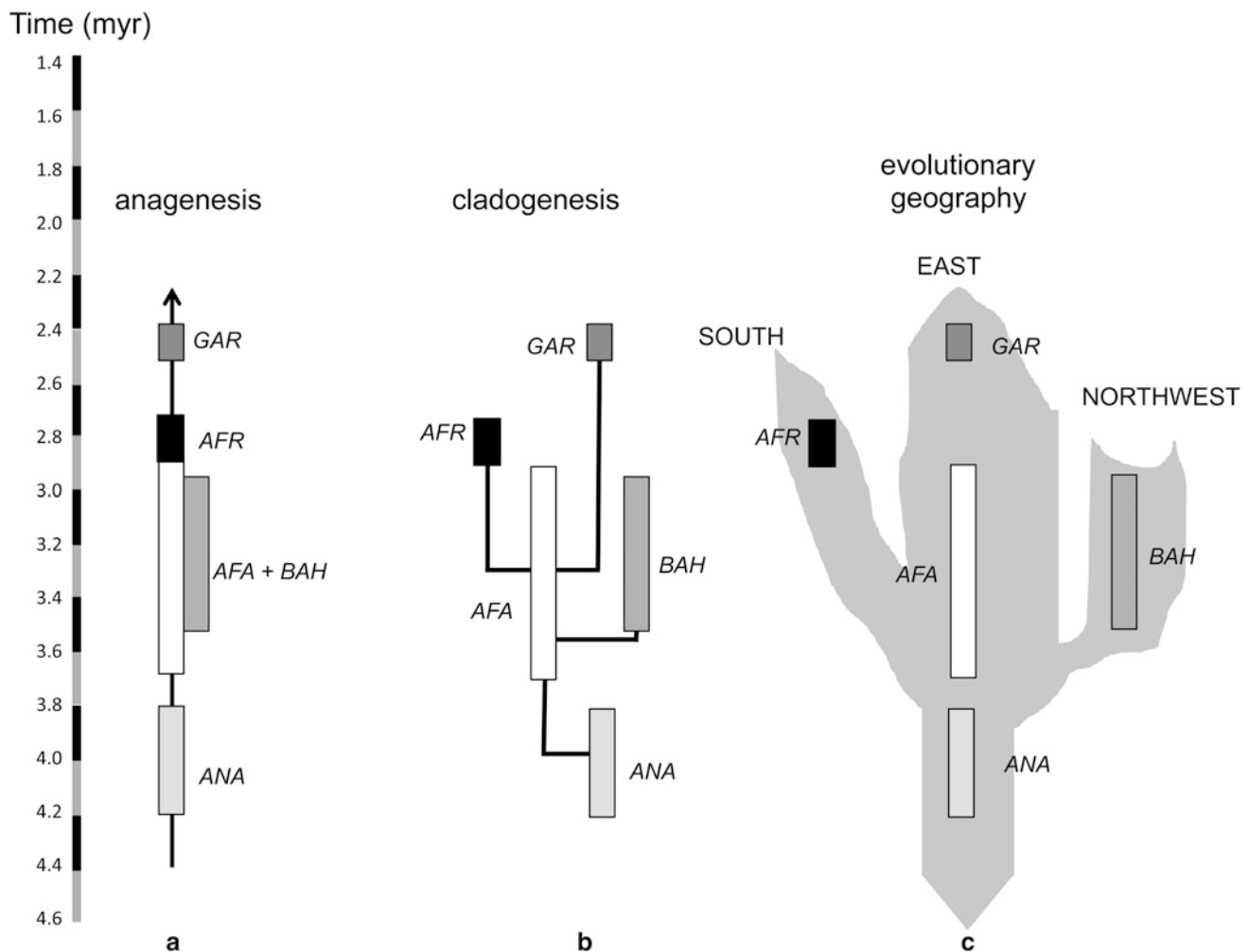


Fig. 10.2 Three views of *Australopithecus* evolution **a** anagenesis; **b** cladogenesis; **c** evolutionary geography. See text for discussion

At one level radiations in evolution are simply shorthand for any form of diversification, and thus all evolution is in some way or other, a radiation. However, there are more formal definitions. According to Schluter (2000), an adaptive radiation is “the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage. It involves the differentiation of a single ancestor into an array of species that inhabit a variety of environments and that differ in the morphological and physiological traits used to exploit those environments. The process includes both speciation and phenotypic adaptation to divergent environments.”

The question is, what is the signal that an adaptive radiation has taken place? Schluter provides four criteria by which we can test whether or not we are dealing with an adaptive radiation:

1. Common ancestry of the component species;
2. Phenotype-environment correlation among the component species;
3. Evidence that there is a trait-utility—i.e., that the features of the component species provide environmentally specific fitness advantages;
4. Rapid speciation.

Placing the australopiths against these criteria is no simple matter. The monophyly is a largely circular argument, as one can use the accepted level of monophyly to determine the component species, rather than the other way around. In the case of the taxa under consideration here, it would probably make no sense to exclude the megadont clades, as all analyses suggest they are derived from an *Australopithecus* species (sensu stricto). However, it is probably also the case that *Homo* should be included as well. Criteria 2 and 3 can be taken together, as the second is essentially an attempt to explain in fitness terms the correlation found under criterion 2. For the australopiths, we know that there are a number of phenotypic differences between the taxa. One approach would be to list the various

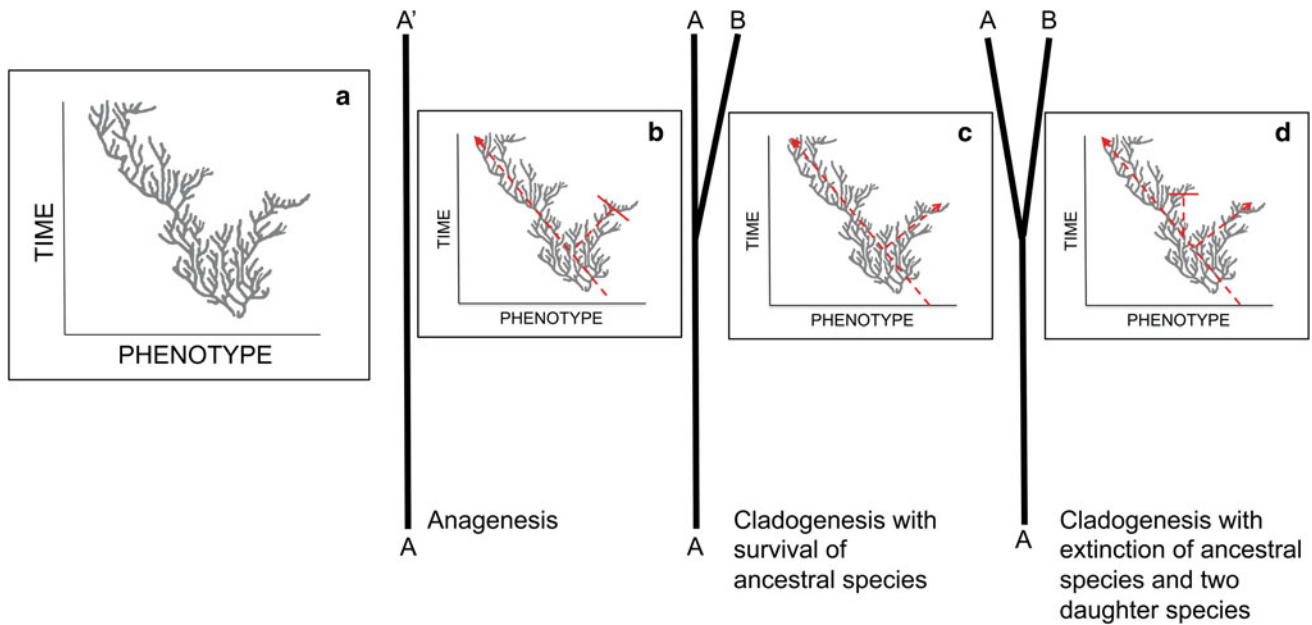


Fig. 10.3 Evolution as cladogenesis. **a** shows how as the phenotype changes or evolves, it is characterised by a process of divergence from the ancestral form, and so is a form of cladogenesis as reticulation declines between populations. In **b–d** different outcomes that can occur are shown—where ancestral “species” becomes extinct, and so

in effect a form of anagenesis has occurred (**b**); where ancestral ‘species’ survives alongside daughter species (**c**); and where cladogenesis occurs and the two daughter phenotypes are different from the ancestral form, which becomes extinct (**d**)

phenotypic traits of the component species (tooth size, body size, brain size, pattern of locomotion, etc.), and then try to correlate these with the known environments. Apart from the problem of the patchy fossil data (what is the EQ of *A. bahrelghazali*?), there is also the problem that the environmental reconstructions of the various taxa overlap considerably—for all the component species, there is general acceptance that the habitats involved a fair degree of tree cover, with patches of bushland and more open grassland (Reed 1997; Behrensmeyer and Reed 2013). Without more precise quantification and better environmental resolution of these, it would be hard to detect a correlation, let alone demonstrate a fitness measure.

In the light of these methodological difficulties, another approach is to consider the question of what is the alternative hypothesis to adaptive divergence. The observation

that we are trying to explain is divergence of a number of lineages from a single one. Two mechanisms can be proposed—one is natural selection and adaptation, which underlies the concept of an adaptive radiation. If this is the mechanism, then there should be an environment-phenotype correlation. The other mechanism would be neutral change, or rather the range of non-adaptive processes which can lead to evolutionary change—drift, founder effect, vicariance, and sexual selection. The expected outcome under this set of mechanisms would be a lack of phenotype-environment correlation. The predictions of each model are shown in Table 10.1.

However, prior to considering these predictions it is necessary to consider whether criterion 4, a necessary precondition, holds. An adaptive radiation is generally considered to be where the ancestral lineage diversifies

Table 10.1 Predictions of distribution of traits under an adaptive radiation model and a neutral diversification model

Prediction	Adaptive radiation model	Neutral diversification model
Relationship between key derived functional traits and the environment	Strong correlation	Weaker correlation
Level of homoplasy	High—due to similar selective pressures in relation to the conditions promoting the radiation	Low—chance effects greater than selection, reducing convergence
Within species variance in key adaptive traits	Low—due to strong selection during speciation for key local adaptive traits	High—reduced effect of local selective processes
Between species variance in key adaptive traits	High—adaptive differences to local conditions promoting inter-population and then species variation	Low—less differentiation in traits between species

relatively quickly, apparently responding to new environmental conditions or the selective benefits of a new adaptation. If that is the case, then the phenotypic differences, and their environmental correlates would indeed be strong evidence for an adaptive radiation. However, if there is not a burst of speciation, but rather a gradual appearance of new species, then it would be difficult to untangle what would, in effect, be evolutionary trends in adaptation, rather than an adaptive radiation.

To explore this possibility, Fig. 10.4 looks at the pattern of “taxon accumulation” across hominin evolution. In the top graph is shown the relative number of *Australopithecus* species which have appeared, plotted against time. The slope of the line will show bursts of speciation. An essential problem here is that the number of taxa are very few (5), and so an alternative is to look at all hominins (excluding the Late Miocene-Early Pliocene ones, which are too poorly known). This is shown in the bottom graph. As can be seen there is a rather continuous pattern of accumulation. The most striking upward trend is between 2.5 and 2.0 Ma, accounted for by the paranthropines (a real adaptive radiation?), and the appearance of early *Homo*.

The absence of a strong signal of rapid speciation among the australopiths might suggest that what is occurring is time transgressive. That, in combination with the absence of sufficient evidence to explore fitness and phenotype-environment relationships, in the context of Schluter’s model of adaptive radiations, provides some insights, but it is far from conclusive. On the whole there is not, in relation to Schluter’s model, a strong adaptive radiation signal among the australopiths. However, we should bear in mind that an adaptive radiation is itself an analytical abstraction; we are not really looking for an event that is or is not an adaptive radiation, but rather, where, on a continuum from simple cumulative divergence, to a full blown explosion of diversification, do the australopiths (and other hominins) fit? While the data tend to indicate an answer closer to the former than the latter, this conclusion is strongly influenced by the selected taxonomic scale—an issue to which I shall return at the end of this paper.

Missing Australopiths and Adaptive Asymmetry

Part of the problem with testing Schluter’s model lies in the fact that the taxonomic scale is relatively small, and it is likely that errors in dating and sampling could have a significant influence on the results. An alternative is to look for another signal of adaptive radiation. Some time ago, Guyer and Slowinski (1993) suggested that the topologies of phylogenies can provide evidence for adaptive radiations.

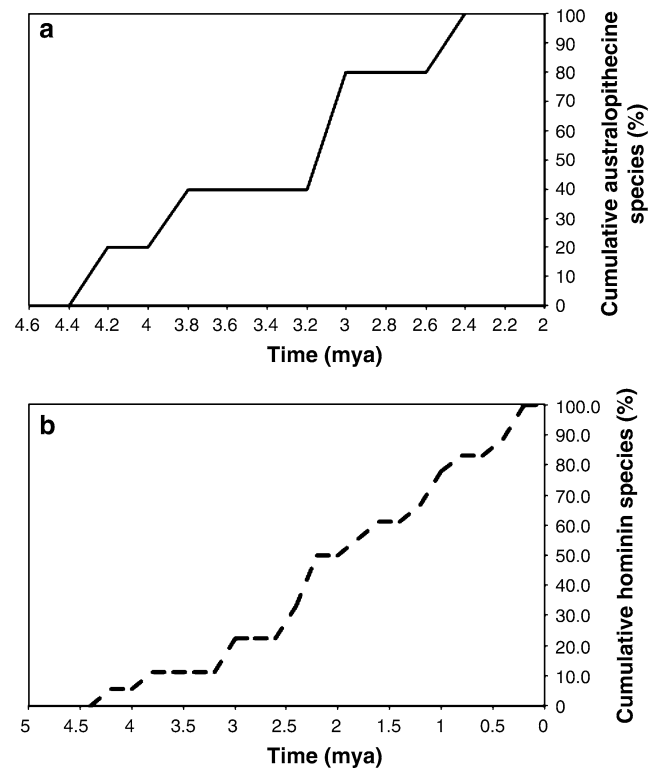


Fig. 10.4 Relative accumulation of new taxon in hominin evolution. The horizontal axis is time in millions of years, and the vertical one shows the percent of the total number of hominin species which have appeared. **a** Australopiths; **b** all post 4.3 Mya hominins

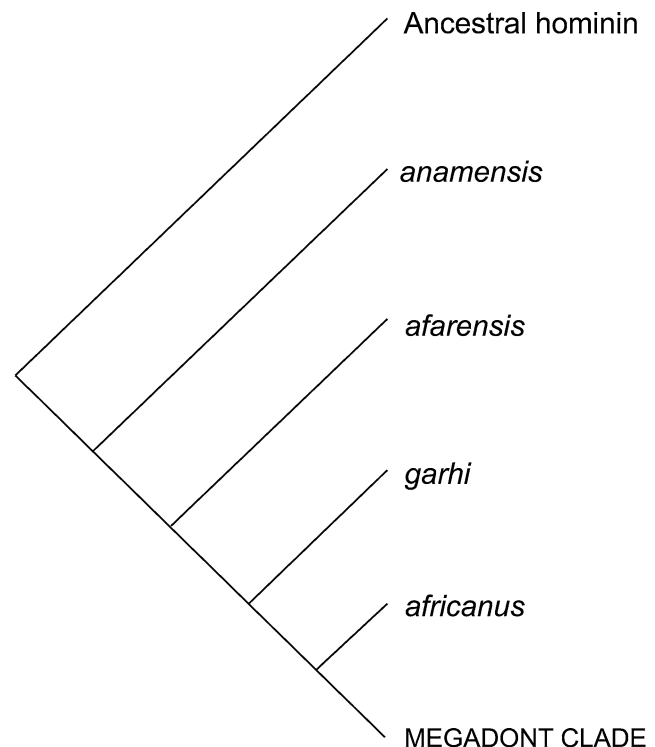


Fig. 10.5 Cladogram of australopith taxa used in text Strait and Grine (2004)

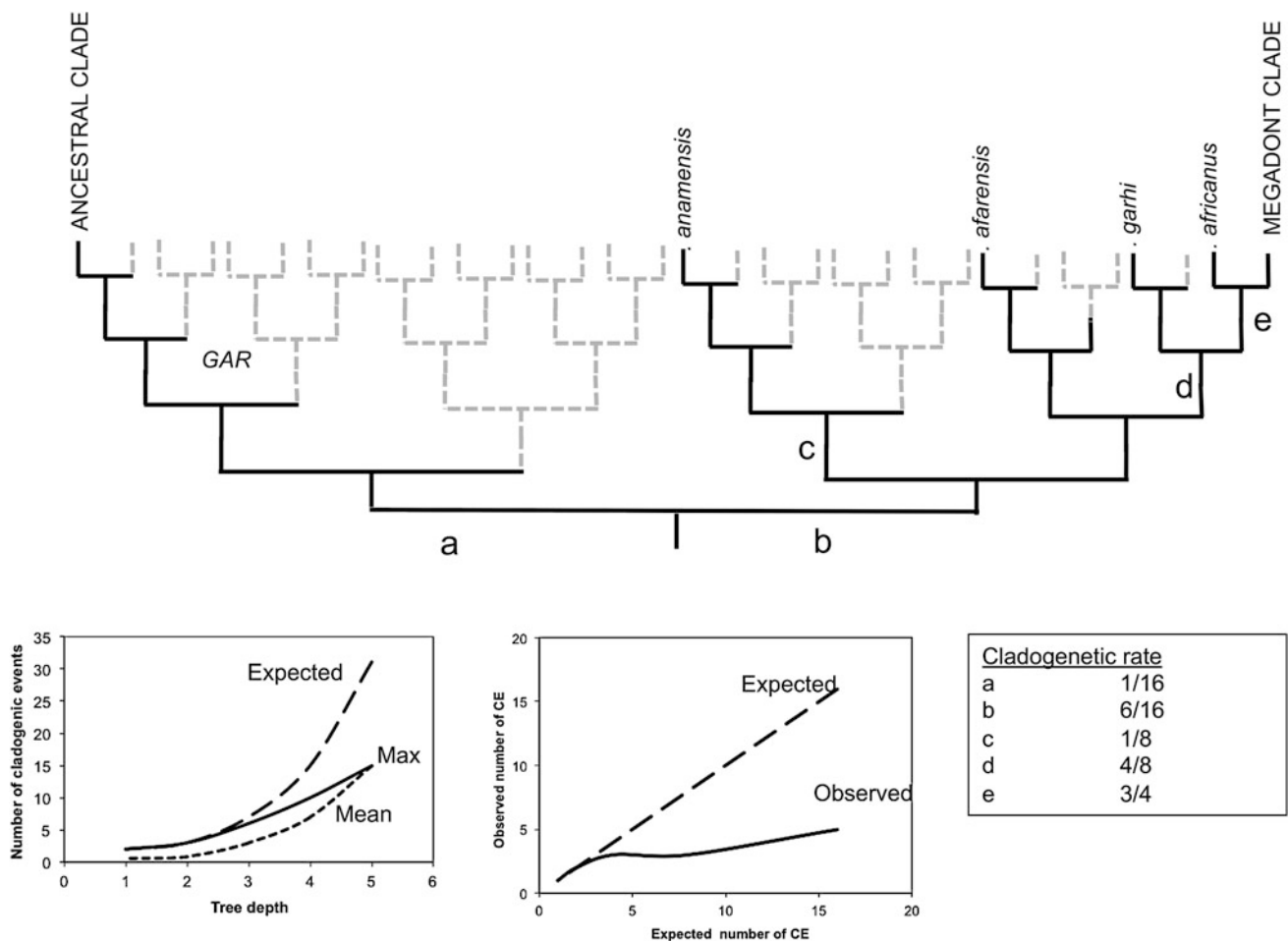


Fig. 10.6 Deviations from the perfect tree. The *top left panel* shows the Equal Rates Markov chain Model for australopiths (known taxa in *black*, "missing taxa" in *dashed lines*). The table at the *bottom right* shows the relative deviation of the *Australopithecus* fossil record from

the model. The graph on the *bottom left* shows the deviation from expected in relation to the depth of the tree, and the graph to the *right* compares observed and expected clades. Right hand table shows the cladogenetic rate for sub clades (letters refer to those in main figure).

Since the publication of their paper there has been considerable progress in this field, and also a multiplication of models (Harcourt-Brown et al. 2001; Bokma 2003; Pineli 2003).

Depending upon scale and taxonomic inclusiveness, the phylogeny of the australopiths is one for which there is broad consensus in general terms, but disagreements about some of the branching sequences. Strait (2013) shows one version, with the entire clade history of hominins until the beginning of the Pleistocene. For the purposes of the analysis here, focusing on the australopiths in a relatively narrow sense, a simplified tree is sufficient to make a theoretical rather than a phylogenetic point (Fig. 10.5). The early hominin phylogenetic tree is a highly odd one—it is strongly asymmetrical. Figure 10.6 illustrates this by showing the same taxa but placed on to an Equal Rate Markov Chain Model tree (with and without the tree pruned (clades shown with dashed line)). What we can see is that

diversification is only apparent on one side of the tree, or, expressed alternatively, there may be a high rate of extinction and low persistence on the other side. Guyer and Slowinski, and subsequently many others, have argued that the degree of asymmetry is a signal of adaptation. Put the other way round, under conditions of neutrality, one can expect Markov Chain processes to occur, and therefore the more asymmetrical the tree, the greater the evidence for adaptation, and thus adaptive radiations.

There are a number of ways of measuring asymmetry. These are mathematically relatively simple, but there are issues relating to analytical artifacts that arise from such things as the taxonomic level. It has also been pointed out that paleontological trees tend to be even more asymmetrical than neontological trees. While this may be expected to be a function of the poor fossil record, it has also been shown that it arises because of the way in which paleontological trees sample across time (Harcourt-Brown et al. 2001).

I have estimated the deviation from that expected under an ERM model (Fig. 10.6) by calculating the ratio of expected to observed clades for different parts of the tree. As can be seen, it is considerable. While this indicates that there are many more taxa out there for us to find, it can perhaps better be interpreted as evidence for adaptive trends, and in the emerging diversity, some trend also towards an adaptive radiation, rather than neutral drift, in the pattern of *Australopithecus* evolution.

A Dispersal Model

Given that there is only a weak signal for an adaptive radiation, we should perhaps ask whether there is a better model for explaining the observed pattern of australopithec evolution. In a previous publication we (Lahr and Foley 1994, 1998) set up a general model of dispersal-based evolution, derived from Tchernov's (1992) geographical perception of the evolution of a lineage. Put simply, the history of a lineage can be described as a series of changes in geographical distribution, from a narrow point of origin, through range expansion(s), to contraction into refugia, and finally, a localised point of extinction. We have used this model extensively to understand the evolution of later *Homo*, but it has also been applied to the Pliocene hominins more generally (Foley 1999). There it was argued that the phylogeny of the early hominins across the Plio-Pleistocene within Africa matched the geographical context, and that the diversity could best be explained in terms of a series of dispersals.

This evolutionary geographical model, adapted for some more recent discoveries, still broadly holds. Rather than develop that element here (but see Strait 2013), instead I want to explore how we might use geographical models to generate new hypotheses. When we think about the geography of African hominins, we are strongly directed towards a simple East versus South perspective, with arrows linking the two (e.g. Lockwood 2013). There is a tendency to add directionality to this, largely from East to South, as this is consistent with chronology, mammalian patterns, and ecological principles (Turner and Wood 1993; Strait and Wood 1999). However, sub-Saharan Africa (and indeed northern Africa too; it should be remembered that the Sahara is by no means a fixed geographical feature) is actually made up of a series of lake basins, river networks, and watersheds. As Kingdon (1984, 1989, 2003) has shown, the evolutionary diversity of mammals is strongly related to these basins, and to the ways in which they respond to climatic change, forming refugia and basins of isolation. Furthermore, their shifts and changes, tectonic or climatic, can form the basis for connectivity as well.

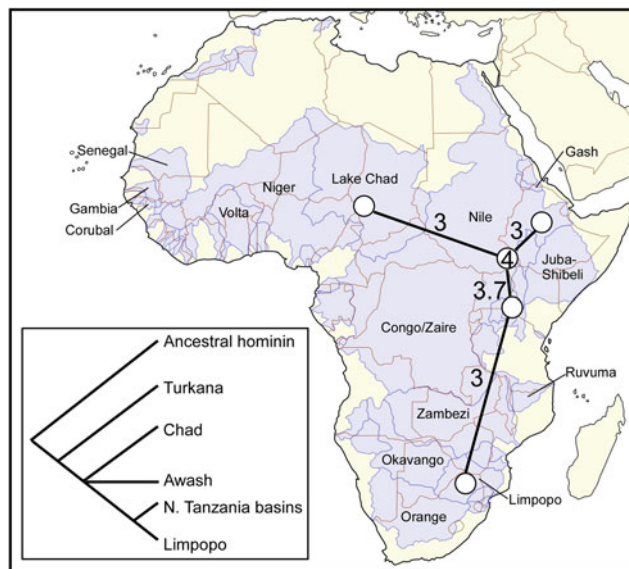


Fig. 10.7 The basins of Africa. The *white circles* indicate basins with australopithec fossils. The *connecting lines* indicate possible routes of connection, with dates in millions of years. The *inset* cladogram shows a “basin-based” cladogram for early hominins

Figure 10.7 shows the basins of sub-Saharan Africa with *Australopithecus* localities superimposed. The first striking thing about these is that there are basins intermediate between those in which hominins are found which would have to be crossed; key ones would be the Nile and the Zambezi, and the Okavango and Rovuma might also be relevant. We can think of our extinct hominins not as species, but more neutrally as paleodemes (Howell 1999), structured by their geography, and the basin structure of Africa can provide the appropriate framework. Links between those basins are created by dispersals and range expansions; differences by subsequent isolation and refugia. Our fossil record is likely to consist of a series of snapshots in that process, repeated over many millennia.

Also superimposed on to the map of the basins are some potential links between the australopithec, with FADs as indicators of a chronology. These links do not replicate the consensus trees, but basins could perhaps be used to generate testable hypotheses, independent of the generally accepted taxa (inset, Fig. 10.7). Further resolution can be added to this by considering distances, numbers of intermediate basins, and paleoenvironmental reconstructions¹—especially as these basins have changed and developed

¹ Figure 10.7 also shows the eastern coastal forest zone, which should more accurately display river systems as well. Kingdon (2003) has suggested that these were crucial to the evolution of bipedal hominins, and played a key role in subsequent diversification, with the river valleys into the interior producing isolation, adaptation, and considerable convergence. They should clearly be considered as both a dispersal route, and as set of north–south barriers in some zones.

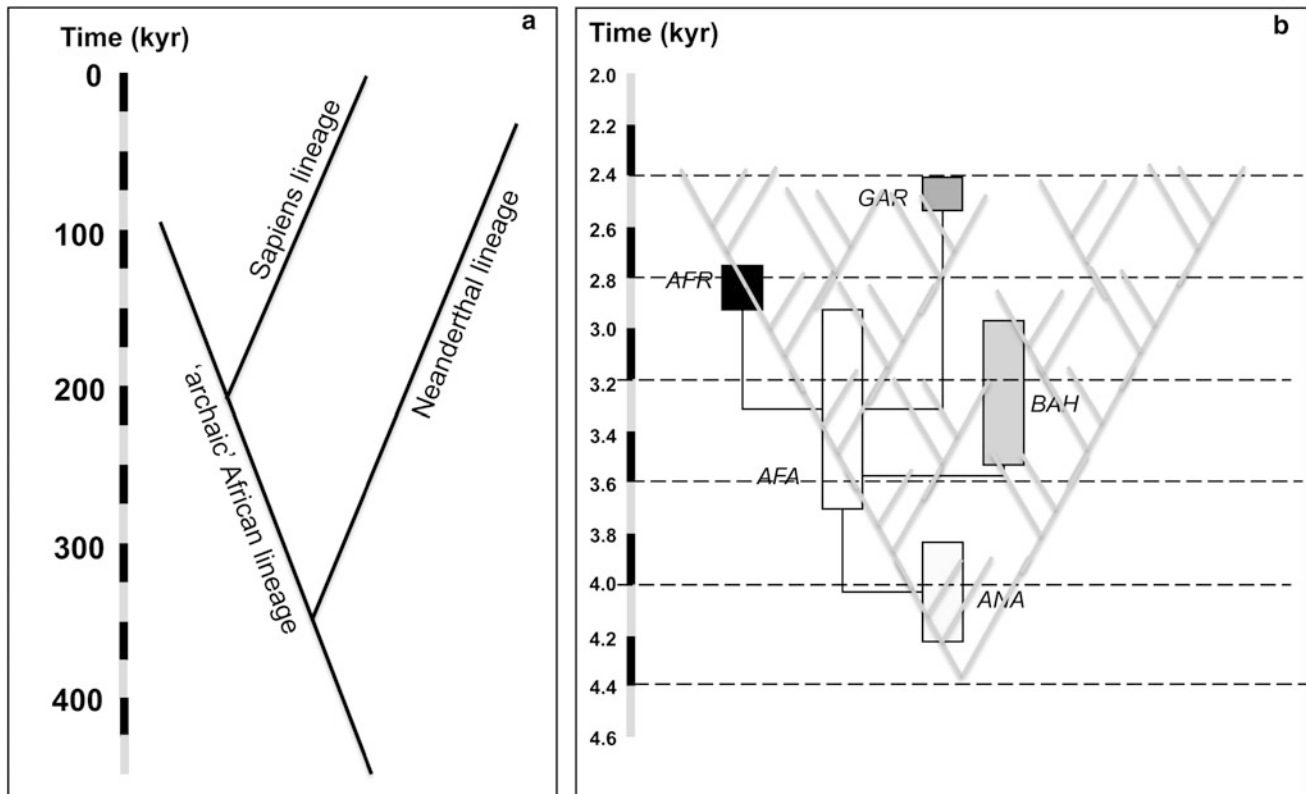


Fig. 10.8 Comparison of evolutionary scale. **a** Shows the evolution of *Homo* over the last 400 kyr. **b** Shows the phylogeny of the australopiths superimposed onto the scale of later *Homo* evolution. Australopith evolutionary scale equates to at least four “later *Homo* events”

considerably over the course of the Pliocene and Pleistocene (e.g., Zambezi, Nile, Congo).

Emerging Problems: Scale

In the models and discussions presented so far one issue that has recurrently been implicit is that of scale. Most of the models and tests that are carried out in the field comparatively consider much larger radiations (vertebrates, birds, cichlids, etc.), where often hundreds of species are involved. The australopiths, and even the hominins as a whole, are a relatively small clade, and so stochastic effects could influence the results rather more than would be the case with large radiations. One example is the analysis of rates of speciation shown above. These are low, and yet it is probably the case that were we to carry out this type of analysis across the whole of the catarrhines, and at a larger chronological scale, bursts of speciation would be more apparent. It is reasonable to ask, therefore, what scale of evolutionary event is represented by the australopiths. To answer this question two comparisons can be made—with the evolution of later *Homo*, and the diversification of *Pan*.

The evolution of later *Homo* is probably the best known diversification event in mammalian evolution, with evidence from genetics, archaeology and fossils. Although this is often characterised as an area of great controversy, in fact we know with considerable precision what happened. Broadly speaking, we can say that over a period of about 450 kyr, hominins diverged into two major lineages, a Eurasian one and an African one (Fig. 10.8a). The Eurasian one evolves into Neanderthals, almost certainly, on the basis of genetic evidence, involving a demographic bottleneck. The African one is diverse, geographically widespread, and also diverges (and presumably speciates), with an ancestral “archaic” population (what we would refer to as *H. helmei* (Lahr and Foley 1998) with a small bottlenecked population evolving into modern humans, and subsequently undergoing a series of major dispersals. The issue here is not the exact phylogenetic details, let alone the question of gene flow, but simply that these two events provide us with a well-documented comparative scale which we can use to examine the australopiths. Essentially we can think of four to five hundred thousand years as a “modern human evolutionary unit” where there is a major continental scale divergence and a geographically smaller divergence within Africa. Figure 10.8b shows the later

Homo “events” superimposed on the *Australopithecus* record, using an equal rate Markov Chain model (ERM). As can be seen, the *Australopithecus* record is, by comparison, rather course-grained. The entire evolutionary history of the australopiths covers four units of later *Homo* evolutionary events. In terms of scale of process, or perhaps more accurately, number of events, the Pliocene is likely to have been much more complex than the models we generally use would imply. This is not to say that there should be another twenty or thirty species to be found, but that, at the demic, sub-species, and lineage divergence level, there are likely to have been far more events.

This comparison has the advantage of making us focus on how the microevolutionary processes which underly a more macroevolutionary pattern can help us explore greater complexity. However, it could be argued, of course, that this is not an appropriate comparison. The reasons for this would include the view that culture-bearing modern humans are completely different, that the scale of climatic variability in the later Pleistocene is higher, or that *Homo* is a global species, whereas the australopiths are confined to a part of Africa. All of these may or may not be true. An alternative comparative framework can therefore be sought in the genus *Pan*. At one level we could simply say that there are three species in *Pan*, and four sub-species, over a period of five or more million years. However, emerging genetic evidence makes it clear that this is an oversimplification. Current estimates would place the divergence of *Pan paniscus* and *Pan troglodytes* at about 800 ka, somewhat younger than previous calculations. The divergence of the most distant of the chimpanzee taxa, *Pan verus* and *P. troglodytes*, is thought to have occurred about 420 ka (Fischer et al. 2004; Won and Hey 2005), and the formation of the other subspecies, somewhat younger. In other words, the current species and sub-species of *Pan* are all relatively recent in the context of the origin of the clade. The observed diversity, in terms of species and sub-species, represents only one fifth of the period since the divergence with the hominins. It is not possible to simply draw these clades back through time; instead we would have to think of a series of (semi?) replacement events, with the *Pan* diversity constantly shifting, albeit with relatively little speciation. The useful insight that can perhaps be used to throw light on the australopiths is that there may be a whole series of dispersals in which, depending on conditions, either previous diversity was erased, or re-organised, and that species are a crude instrument for measuring this.

One way of looking at the diversity of *Pan* as a model for hominin evolution is that it would lead to a rather more conservative view of diversity than the later *Homo* model, albeit still a complex one. However, there is another element to which it is worth drawing attention. While there is no evidence for gene flow between *P. paniscus* and

P. troglodytes, there is within *P. troglodytes*. According to Won and Hey (2005), this flow is primarily from west to east, suggesting a recurrent directionality that will produce a level of sub-species asymmetry. Eastern chimpanzees will accumulate traits of their own, but also absorb novelties from the west. This might be a factor in differential levels of variation, conservatism, and apomorphies among australopiths, where instead we are likely to be looking at north–south/south–north patterns.² We tend to think of dispersals as events with directions, but these results show that gene flow can also have strong biogeographical directionality.

Discussion

This paper started by accepting the challenge of exploring the idea that there was an australopith radiation. This led to a consideration of one or two of the formal models that have been developed more broadly to determine whether evolutionary patterns are adaptive radiations. While there is a clear signal in the tree asymmetry of the australopiths, other signals were more ambivalent. The primary theoretical conclusion was that if our question relates to the patterns and processes of divergence, then there is a continuum from simple dispersal driven divergence to explosive speciation. *Australopithecus* species, and probably all hominins, are likely to be closer to the former than the latter, but nonetheless, are moderately speciose.

An alternative approach was to consider the australopith diversity as a product of dispersal under an evolutionary geography model. This showed that there is broad congruence between geographical patterns and the australopith (and robust australopith) probable dispersals. In order to develop this approach it was proposed that biogeographic basins could be used as a framework for phylogenetic analysis, and developing new hypotheses that were not necessarily based on current species designations.

Some general conclusions about the australopith radiations are:

1. Dispersals are the driving force in diversification following the evolution of “a new trick” (bipedalism?) and/or changes in environment.
2. Adaptively driven diversification of the phenotype following dispersal will be dependent upon the level of environmental variation and the degree of specialisation of the lineage (this is similar to Vrba’s 1992, effect hypothesis which explained, for example, why impala speciated at a much slower rate than alcelaphines under

² Interestingly enough, among gorillas the gene flow appears to be stronger from east to west (Thalmann et al. 2007).

similar conditions). For the australopithecines it is likely that there was a broad similarity of habitat, and a lack of extreme specialisation as large bodied primates.

3. The outcome was a moderate level of speciation and diversification, of which we are picking up only a small proportion under the basin model proposed.
4. Adaptive radiations where there are very high levels of speciation tend to be associated with high levels of sexual selection (e.g., among passerine birds high rates of speciation are associated with levels of plumage colouration (cf. cercopithecines)), and perhaps we can infer this is not the case for early hominins.
5. The scale of the australopithecine ‘radiation’ is perhaps rather limited, but when the more general comparative models derived from larger studies are grounded against either recent hominins or African apes, we should perhaps still expect considerably more diversity to occur, although within limited phenotypic ranges.

This paper has explored the australopithecines in the light of various general evolutionary models. Many might say that we are better off being strictly empirical. However, all empirical studies are bounded by theories and models, and it is better to make them explicit rather than leave them unspoken. More importantly, unless we know what to expect in evolutionary history, it is very difficult to understand what it is we have observed (see Ezard et al. 2011, for a demonstration of this in relation to mammalian evolution more generally). There are, across the evolutionary field, many powerful models which can be used to investigate patterns of human evolution. But perhaps my strongest argument in favour of more theory in paleoanthropology is a completely different and surprising one. Although we all complain about the problems of the fossil record, hominin evolution is a remarkably well-studied and data rich field. The pattern of human evolution can be used to test and develop general models in evolutionary biology.

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References

- Behrensmeier, A. K., & Reed, K. E. (2013). Reconstructing the habitats of *Australopithecus*: Paleoenvironments, site taphonomy, and faunas. In K. E. Reed, J. G., Fleagle, & R. E. Leakey (Eds.), *The paleobiology of Australopithecus* (pp. 41–60). Dordrecht: Springer.
- Berger, L. R., Lacruz, R., & de Ruiter, D. J. (2002). Revised age estimates of *Australopithecus*-bearing deposits at Sterkfontein, South Africa. *American Journal of Physical Anthropology*, *119*, 2–197.
- Berger, L. R., deReuter, D. J., Churchill, S. E., Schmid, P., Carlson, K. J., Dirks, P. H. G. M., et al. (2010). *Australopithecus sediba*: A new species of *Homo*-like australopithecine from South Africa. *Science*, *328*, 195–204.
- Bokma, F. (2003). Testing for equal rates of cladogenesis in diverse taxa. *Evolution*, *57*, 2469–2474.
- Clarke, R. J. (2013). *Australopithecus* from Sterkfontein Caves, South Africa. In K. E. Reed, J. G. Fleagle, & R. E. Leakey (Eds.), *The paleobiology of Australopithecus* (pp. 105–123). Dordrecht: Springer.
- Conroy, G. C. (2002). Speciosity in the early *Homo* lineage: Too many, too few, or just about right? *Journal of Human Evolution*, *43*, 759–766.
- de Ruiter, D. J., Churchill, S. E., & Berger, L. R. (2013). *Australopithecus sediba* from Malapa, South Africa. In K. E. Reed, J. G., Fleagle, & R. E. Leakey (Eds.), *The paleobiology of Australopithecus* (pp. 147–160). Dordrecht: Springer.
- Eldredge, N., & Cracraft, H. (1980). *Phylogenetic Patterns and the Evolutionary Process*. New York: Columbia University Press.
- Fischer, A., Wiebe, V., Paabo, S., & Przeworski, M. (2004). Evidence for a complex demographic history of chimpanzees. *Molecular Biology and Evolution*, *21*, 799–808.
- Fleagle, J. (1999). *Primate adaptation and evolution*. New York: Academic Press.
- Foley, R. A. (1987). *Another unique species: Patterns of human evolutionary ecology*. Harlow: Longman.
- Foley, R. A. (1991). How many hominid species should there be? *Journal of Human Evolution*, *20*, 413–427.
- Foley, R. A. (1999). The evolutionary geography of Pliocene hominids. In T. Bromage, & F. Schrenk (Eds.), *African biogeography, climatic change, and hominid evolution* (pp. 328–348). Oxford: Oxford University Press.
- Foley, R. (2002). Adaptive radiations and dispersals in hominin evolutionary ecology. *Evolutionary Anthropology*, *11*, 32–37.
- Grine, F. E. (2013). The alpha taxonomy of *Australopithecus africanus*. In K. E. Reed, J. G., Fleagle, & R. E. Leakey (Eds.), *The paleobiology of Australopithecus* (pp. 73–104). Dordrecht: Springer.
- Guyer, G., & Slowinski, J. (1993). Adaptive radiation and the topology of large phylogenies. *Evolution*, *47*, 253–263.
- Harcourt-Brown, K. G., Pearson, P. N., & Wilkinson, M. (2001). The imbalance of paleontological trees. *Paleobiology*, *27*, 188–204.
- Howell, F. C. (1999). Paleo-demes, species clades, and extinctions in the pleistocene hominin record. *Journal of Anthropological Research*, *55*, 191–243.
- Hunt, K. D. (2003). The single species hypothesis: Truly dead and pushing up bushes, or still twitching and ripe for resuscitation? *Human Biology*, *75*, 485–502.
- Jacob, F. (1977). Evolution and tinkering. *Science*, *196*, 1161–1166.
- Kimbel, W. H., Lockwood, C. A., Ward, C. V., Leakey, M. G., Rak, Y., & Johanson, D. C. (2006). Was *Australopithecus anamensis* ancestral to *A. afarensis*? A case of anagenesis in the hominin fossil record. *Journal of Human Evolution*, *51*, 134–152.
- Kingdon, J. (1984). *East African mammals: An Atlas of evolution in Africa*. Chicago: University of Chicago Press.
- Kingdon, J. (1989). *Island Africa*. London: Academic Press.
- Kingdon, J. (2003). *Lowly origin: Where, when, and why our ancestors first stood up*. Princeton: Princeton University Press.
- Lahr, M. M., & Foley, R. A. (1994). Multiple dispersals and modern human origins. *Evolutionary Anthropology*, *3*, 48–60.
- Lahr, M. M., & Foley, R. A. (1998). Towards a theory of modern human origins: Geography, demography, and diversity in recent human evolution. *Yearbook of Physical Anthropology*, *41*, 137–176.
- Lockwood, C. (2013). Whence *Australopithecus africanus*? Comparing the skulls of South African and East African *Australopithecus*. In K. E. Reed, J. G., Fleagle, & R. E. Leakey (Eds.), *The paleobiology of Australopithecus* (pp. 175–182). Dordrecht: Springer.

- Partridge, T. C., Granger, D. E., Caffee, M. W., & Clarke, R. J. (2003). Lower Pliocene hominid remains from Sterkfontein. *Science*, *300*, 607–612.
- Pineli, I. (2003). Evolutionary models of phylogenetic trees. *Proceedings of the Royal Society B*, *270*, 1425–1431.
- Reed, K. E. (1997). Early hominid evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution*, *32*, 289–322.
- Schluter, D. (2000). *The ecology of adaptive radiations*. Oxford: Oxford University Press.
- Spoor, F., Leakey, M. G., Gathogo, P. N., Brown, F. H., Antón, S. S., McDougall, I., et al. (2007). Implications of new early *Homo* fossils from Ileret, east of Lake Turkana, Kenya. *Nature*, *448*, 688–691.
- Stanley, S. M. (1992). An ecological theory for the origin of *Homo*. *Paleobiology*, *18*, 237–257.
- Strait, D. S. (2013). The biogeographic implications of early hominin phylogeny. In K. E. Reed, J. G., Fleagle, & R. E. Leakey (Eds.), *The paleobiology of Australopithecus* (pp. 183–191). Dordrecht: Springer.
- Strait, D. S., & Grine, F. E. (2004). Inferring hominoid and early hominid phylogeny using craniodental characters: The role of fossil taxa. *Journal of Human Evolution*, *47*, 399–452.
- Strait, D. S., & Wood, B. A. (1999). Early hominid biogeography. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 9196–9200.
- Tchernov, E. (1992). Dispersal: A suggestion for a common usage of this term. *Courier Forschungsinstitut Senckenberg*, *153*, 21–25.
- Thalmann, O., Fischer, A., Lankester, F., Paabo, S., & Vigilant, L. (2007). The complex evolutionary history of gorillas: Insights from genomic data. *Molecular Biology and Evolution*, *24*, 146–158.
- Turner, A., & Wood, B. A. (1993). Taxonomic and geographic diversity in robust australopithecines and other Plio-Pleistocene mammals. *Journal of Human Evolution*, *24*, 147–168.
- Vrba, E. (1985). Ecological and adaptive changes associated with early hominid evolution. In E. Delson (Ed.), *Ancestors: The hard evidence* (pp. 63–71). New York: Alan Liss.
- Vrba, E. S. (1992). Mammals as a key to evolutionary theory. *Journal of Mammalogy*, *73*, 1–28.
- White, T. D. (2003). Another perspective on hominid diversity—response. *Science*, *301*, 763–764.
- White, T. D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C. O., Suwa, G., et al. (2009). *Ardipithecus ramidus* and the paleobiology of early hominids. *Science*, *326*, 64–86.
- Won, Y.-J., & Hey, J. (2005). Divergence population genetics of chimpanzees. *Molecular Biology and Evolution*, *22*, 297–307.
- Wood, B., & Collard, M. (1999). The changing face of genus *Homo*. *Evolutionary Anthropology*, *8*, 195–207.