

3 Pattern and process in hominid evolution

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Summary

Explanations in evolution generally, and human evolution in particular, vary in the extent to which emphasis is placed on adaptation or on other factors, such as chance or historical contingency. In this paper the broad pattern of hominid evolution above the species level is described and used to throw light on the processes of evolution involved. Adaptive radiations, species survivorship, biogeographical patterns and the relationship with climatic change all show that chance and historical contingency play a role in the formation of the initial conditions under which evolution occurs, but that the detailed micro-evolutionary shape of any outcome is a function of adaptation and selective mechanisms.

Introduction

The development of the theory of natural selection and the widespread acceptance of evolution in biology is usually treated as a watershed in biological thought. As has often been discussed (Bowler, 1989), the innovation of Darwin and Wallace was not so much the proposal that evolution had occurred, but their specific mechanism for accounting for its occurrence and pattern. That theory – differential reproductive success leading to changes in gene frequencies resulting in better adapted organisms and populations – tipped the balance of a long-standing debate over

what shapes plants and animals. Darwin placed the emphasis on function, hence the key role of adaptation in neo-Darwinist theory; organisms are the way they are because of the requirements of their environment, through the mechanism of natural selection.

Historically, alternative theories placed the stress on other factors. One such was the idea of archetypes, which in modern biological terms equates to the constraints of structure and development: organisms are the way they are because there are only a limited number of ways in which 'biological design' can be implemented. The rise and triumph of Darwinism has not necessarily seen the disappearance of all other factors in evolution other than natural selection. Indeed, debates within evolutionary biology revolve primarily around the relative significance of natural selection and the way in which this mechanism interacts with others. The primary alternative candidates remain much the same as in the nineteenth century (see Gould's Introduction, p. xiv) – the constraints of development on adaptive design, and the effect of past events – 'history' on subsequent evolutionary pathways. It is these factors that make evolutionary events, and the operation of natural selection, contingent. The question that arises for human evolution, therefore, is the significance of contingency in the evolution of one particular lineage. More specifically, how can we balance explanations that stress function in evolution, and those that stress contingent factors. Here I shall look at the overall pattern of hominid evolution to see what can be inferred about process, and in particular the relative roles of adaptation and other, more contingent, factors.

Species in human evolution

A first problem that arises is the extent that human evolution is a single lineage. Conventionally, since the more rigorous application of the rules of zoological nomenclature and the widespread acceptance of the biological species concept, human evolution has largely been treated as anagenetic in character, involving a limited number of taxa, and consisting primarily of an expansion in the size of the brain. Much of the rest of palaeoanthropology could largely be considered to be concerned with the minutiae of anatomy.

It is clear that this is no longer the case. When Mayr (1950) pruned the human evolutionary tree he reduced it to three basic species – *Australopithecus africanus*, *Homo erectus* and *Homo sapiens*, with a possible fourth in the form of a more megadontic species, *A. robustus*. Since that time there has been a steady upward drift in the number of recognized hominid species. Pilbeam's (1972) widely read synthesis added *H. habilis* and gave stronger credence to the

robust australopithecine. Howell (1978) split the robust australopithecines to add further taxa, resulting in eight. Groves (1989), using a formal phylogenetic analysis, proposed sixteen species, while a recent survey by Wood (1991, 1995) suggested thirteen species. Foley (1991) argued that there were a maximum of nineteen known species in the hominid fossil record.

This increase in taxonomic diversity among the hominids has been partly a result of the relentless discovery of new species of hominid, of which *Ardipithecus ramidus* is but the most recent (White et al., 1994), principally in Africa, over the last three decades. It has also been affected by the increased use of cladistics, which both requires more species for analysis to be possible, and depends on defining taxa at the outset of the analysis. Where multivariate statistics tended to stress overlap between hominid morphologies, cladistics works best by emphasizing differences.

Now the rise in the number of taxa is significant because it means we are not dealing with a straightforward anagenetic or simple linear evolutionary process, and therefore we can start to compare different hominid species. Evolutionary biology is essentially a comparative subject, and having several species allows the comparison of different hominids adaptively as well as simply in terms of gradual transitions from one to another. Each of these species will have a specific point of origin, time of last appearance, and by calculation, a longevity or duration – the time elapsed from appearance to disappearance. This type of data (Figure 3.1) allows us to talk about more general evolutionary processes – extinction and speciation – in ways that are comparable with palaeontologists and evolutionary biologists working on other lineages distant from humans.

Hominid evolution as a pattern of adaptive radiations

The advantage of treating hominid evolution as a constellation of species, rather than an evolving lineage, is that we can ask what are the causes of evolutionary change in general, the patterns and processes of human evolution. What causes speciation and extinction? How long do hominid species survive? What are the patterns of diversity? Do hominid species coexist and if so, how do they interact? This last question is important in broad terms, for it is an area for which we have few models. *Homo sapiens* is the sole surviving species, and so we know little about the way in which a human or hominid would interact with a closely related species.

The first such observation is that, with the multiple species and contemporary species observable in Figure 3.1, the pattern of

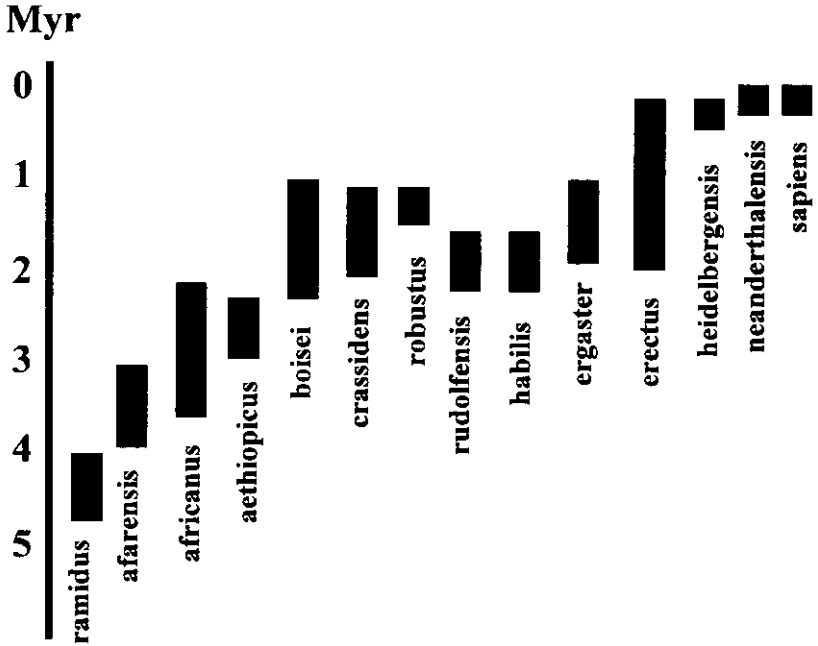


Figure 3.1 Species in human evolution

hominid evolution can be described as a series of adaptive radiations. An adaptive radiation is when there is a diversification of lineages from an ancestral lineage – in other words the multiplication of closely related taxa, usually linked by a common set of characteristics and adaptations. Three such radiations can generally be recognized (Figure 3.2): that of the early bipeds from around 4 Mya (*A. ramidus*, *A. afarensis*, *A. anamensis*, *A. bahrelgazali*, *A. africanus*); that of the megadontic robust australopithecines (*A. aethiopicus*, *A. boisei*, *A. robustus*, *A. crassidens*); and that of the more encephalized *Homo* (*Homo habilis*, *H. rudolfensis*, *H. ergaster*, *H. erectus*, *H. rhodesiensis*, *H. heidelbergensis*, and *H. neanderthalensis*). A fourth is shown here – the spread of *Homo sapiens* (AMH), but this is fundamentally different in not involving biological diversification to anything like the extent seen in the other ones. The radiation of *Homo sapiens* is one of geographical dispersal, and is significant for its behavioural implications.

In terms of the processes of evolution involved, the occurrence of multiple species within the hominids and the pattern of adaptive radiations is significant in that it conforms to that found in other groups of animals. Adaptive radiations are the norm of

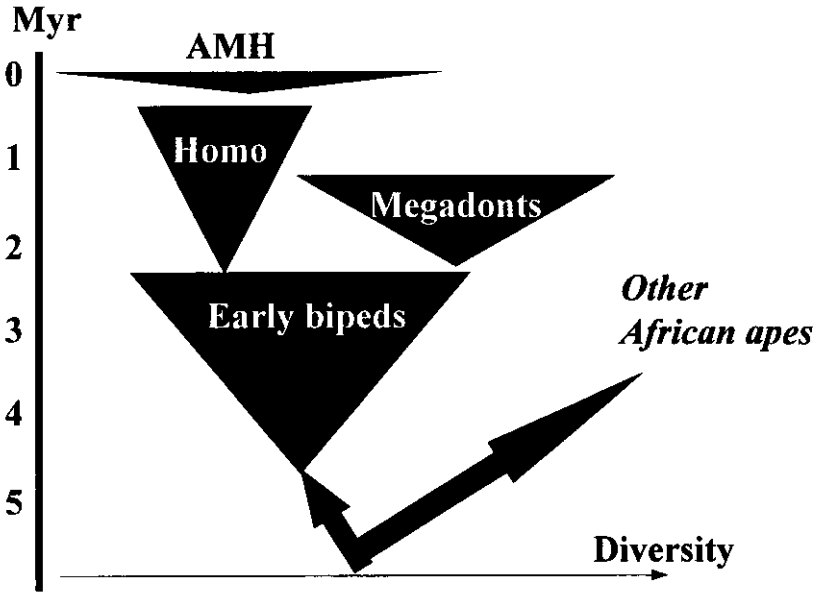


Figure 3.2 Hominid evolution as a pattern of adaptive radiations

evolutionary biology. New forms evolve, and then radiate and diversify to fill a range of ecological niches and geographical positions, and then they will gradually dwindle and decline through extinction, resulting in a loss of diversity. The shape of hominid evolution is the same as the shape of that of any other group, and there is nothing very special at this level (Foley, 1987, 1995b). It might therefore be possible to infer that the mechanisms and processes underlying hominid evolution are not qualitatively different from those of other species.

What of the roles of adaptation and more contingent factors in these adaptive radiations? In one sense they are clearly the result of contingency: the evolution of bipedal apes in Eastern Africa five million years ago is contingent upon the effects that rifting activity had upon the climates of Africa, and contingent upon the presence of large-bodied suspensory hominoids in adjacent or relict arboreal habitats. The geographical radiation of *Homo* was contingent upon the climatically determined shifts in both sea level and habitat distributions. Different abiotic and phylogenetic circumstances would undoubtedly have produced different evolutionary outcomes. However, while the timing and location of evolutionary events may be contingent upon the historical situation, it is clear

that the way in which the evolutionary responses are played out is a function of other mechanisms. It is here that the role of natural selection becomes clear. Given certain initial conditions, the outcome will be the product of competitive interactions between individuals, populations and species, in which those organisms best suited to the conditions will have a reproductive advantage. In this way characteristics such as bipedalism or increased meat-eating, characteristics that underlay the hominid adaptive radiations, are adaptive, functional, and the product of natural selection.

The survivorship of species

From the ten or more species of hominid that have existed, only one is still in existence. The unitary nature of the human species is itself an interesting problem, as is the question of when hominids last occurred in multiple species. However, from the point of view of the pattern and process of hominid evolution, one useful approach is to consider how long hominid species survive. Is it a matter of chance which species survive, and which ones become extinct? Are there patterns to survivorship within the hominid lineage? Using Gould's (1989) metaphor, were the tape to be replayed, would the outcome be the same, or would the Neanderthals have replaced modern humans, or the robust australopithecines survived through to the present day, where we might watch them chewing away in London Zoo? Certainly it is an interesting observation, since two million years ago the robust australopithecines appear to be far more abundant in the fossil record than early *Homo* (Wood, 1991).

The average longevity of a mammalian species is around one million years (Stanley, 1978). Species longevity can be very crudely estimated by subtracting the date of last appearance in the fossil record from the date of first appearance. When this analysis is carried out for hominids, it appears that the average longevity is close to the mammalian average of one million years (Foley, 1993). Again, this supports the view that hominid evolution, in pattern at least, is similar to that of other mammalian groups. The average duration, however, hides considerable variation. Some taxa, such as *Australopithecus africanus* and *A. afarensis* have longevities that exceed one million years, while the 'species' of *Homo* are all rather short-lived. Our own species, *Homo sapiens*, has been in existence for little more than 100 kya, and Neanderthals lasted as a species for not much longer than this.

This variation may tell us something about pattern and process. One observation is that species turnover increases during the course of hominid evolution. The tempo of evolutionary change is

accelerating. This may be due to a number of factors – the increased rate of climatic change (but see below), or the autocatalytic effect that human behaviour had on evolutionary rates, or the greater diversity of habitats occupied as hominids became more global in distribution. However, it may also be the case that what is taken to be a species becomes increasingly suspect in the later parts of human evolution, and therefore the results are an artefact. Even artefacts are interesting, though, and the problematic nature of the species concept in later human evolution might be itself an indication of a changing set of processes – a greater role for behavioural mechanisms or the relatively rare problems associated with pan-global distributions.

In terms of inferring process, a study of species survivorship is informative. Perhaps the most interesting point is that while at the level of the family as a whole there are regularities that lead to hominids converging on the mammalian mean, each of the events underlying it is a response to unique conditions and chance events. In other words, if several factors are operating – and they may be contingent, stochastic or strongly deterministic and functional – the macro-patterns will not reflect the variability in the underlying causes. Macro-evolution will not reflect micro-evolution (see Paul, this volume).

The geography of hominid evolution

If we accept that hominid evolution is not a simple linear process, the ladder of progress up towards modern humans, but actually a series of adaptive radiations, then one of the implications is that the hominid lineage has undergone speciation, that new species have arisen. This observation takes us into one of the most controversial areas in evolutionary biology – what promotes speciation? Under what conditions do new species arise? Do new species always arise through cladogenesis? Rather than pursue the complexities of speciation theory here, I will look at the patterns of speciation among the Hominidae, to see if this can throw light on the conditions under which new hominid taxa have emerged.

A starting point might be the patterns of speciation found in non-human primates. The catarrhines (Old World monkeys and apes) show a clear trend – where a genus is distributed over a large area, there will be a large number of species. In other words, new and more species will occur as geographical range increases (Foley, 1991). This is consistent with an allopatric model of speciation: as populations disperse, and cover a larger area, a greater number of geographical barriers, or other barriers to reproduction, start to occur; in addition adaptation to different environments will

promote differences between populations. Divergence – or speciation – is a response to geographical dispersal.

If we look at hominid evolution in geographical rather than chronological terms, we can use models derived from the catarrhines to see whether new hominid species occur in response to geographical dispersal in the same way as other catarrhine species.

The details of this analysis have been presented elsewhere (Foley, 1991). The principal points that emerge are that during the earlier part of hominid evolution, that is when the australopithecines and early *Homo* occurred only in parts of sub-Saharan Africa, the number of species observable in the fossil record (between 6 and 10) conforms to the number predicted by the catarrhine model. Speciation among early hominids is both relatively common and occurs at about the rate that would be expected for an ape. However, as hominids expanded out of Africa between two and one million years ago, the number of taxa did not increase markedly. The model would predict more than 20 species of later Pleistocene hominid, whereas even the most rampant splitter is unlikely to recognize more than four or five, and two or three is far more probable. For later hominid evolution, patterns of speciation do not fit the primate-based model, and one might infer that different mechanisms are occurring.

A further comparison is illuminating here. Other groups have very low rates of speciation in response to broad geographical distributions, of which the best examples are the large carnivores. Not only does the species concept not work very well for these groups, as was the case for later hominid evolution (see above), so too it appears that they are able to disperse very widely without speciation.

In other words early hominids are speciating like typical catarrhine primates, but later hominids are behaving more like carnivores. What does this tell us in terms of evolutionary process? Two points should perhaps be highlighted. The first is that if we think about why geographical dispersal should lead to speciation, the answer lies in the formation of geographical barriers, separating parent and daughter populations. Such barriers are usually (although not exclusively) abiotic, and thus the conditions for speciation are independent of the vectors of selection. Contingency – unpredictable initial conditions – therefore underlay the fundamental mechanisms of evolutionary divergence. The second point, however, is in contrast to this. Both primates and large carnivores have dispersed widely and met barriers; their response, though, has been very different. The differences are due to the

adaptive differences between the groups – carnivores are more tolerant of resource and habitat variation than the primarily herbivorous primates. Once again response to novel circumstances, therefore, is strongly influenced by initial conditions which are partly stochastic, but the final outcomes are the result of strongly deterministic forces. In hominid evolution it appears that there is a change in those deterministic forces – selection – that occurs in later hominid evolution, possibly as a response to increased meat-eating, that affects the pattern of subsequent hominid evolution.

Climate and hominid evolution

The interaction between biotic and abiotic, stochastic and deterministic, adaptive and historical factors that has underlain this discussion of processes in human evolutionary biology, has been tangentially tackling the issue of causality in evolution. A related issue is whether evolution is dependent upon external environmental change, or whether there is a purely biological dynamic involved. The testing ground for this debate is the relationship between climatic change and human evolution. Why do particular species appear at particular times? Is it a product of climatic change?

The most powerful model for a driving force in hominid evolution is a climatic one. Vrba (1985) suggested a relationship between the split from *Australopithecus* to *Homo* and the climatic deterioration that occurred at around 2.4 million years. Suggestions for other climatic events, such as one affecting the origins of *H. sapiens*, have also been made. These are particular events in hominid evolution, but now that a large number of taxa have been identified it is possible to develop a quantitative test of the more general proposition that climatic change is a necessary cause of speciation. Again, the results of these analyses have been presented elsewhere (Foley, 1994); here it is the general implications that are significant. The primary finding of an examination of the relationship between hominid and baboon speciation and climatic change in a number of variables (average temperature, climatic stability, etc.) showed no significant effect. Even when extended to other mammalian groups, the only species that seemed to be directly sensitive to climatic change were the African bovids. This remained true at different scales of chronological resolution and temporal lagging. While there is no relationship between the appearance of new species and climate, there is a weak one between climate and extinction.

The conclusion to be drawn is that climate does not directly drive evolutionary change. Evolutionary change can occur without any climatic change, and equally climate can change without any

apparent evolutionary effects. Again, the pattern of hominid evolution can throw light on the processes. It appears that external environmental change has the most direct effect on rates of extinction. This is much as would be expected, through such mechanisms as habitat loss and fragmentation. How new taxa respond through evolutionary change and speciation, though, is subject to a far greater number of factors. The link is far more indirect, and in particular local demographic and competitive conditions are bound to play a major role. Once again, to understand evolution it is necessary to return to the small scale and the local, and there the role of selection, competition and adaptation is likely to be significant. Evidence for this view is perhaps to be found by looking at what is actually evolving among the hominids. There is increasing evidence that during early hominid evolution at least there was considerable parallel evolution – that is, the same characteristics evolved independently in more than one lineage. Megadonty, for example, the key trait of the robust australopithecines, may have evolved three times (Skelton and McHenry, 1992) and Wood (1991) has shown that homoplasies are rife in the early hominid evolutionary record. Convergence is perhaps the strongest evidence for adaptation, and indicates that despite the contingent factors that lie at the base of evolutionary episodes, the rules of survivorship and reproductive success govern the final outcome (Foley, 1995a).

Conclusion

A number of general points have been made about the processes underlying human evolution on the basis of the pattern that we can observe in the fossil record. The first of these was that the pattern of hominid evolution is similar to that of other mammalian lineages, and therefore it is likely that the mechanisms are similar too. The second was that while contingency plays a part in the timing and location of evolutionary events, the way those events are played out, the final biological outcomes, are strongly influenced by selection, adaptation and function. In this sense discussions about the roles of selection versus other factors in evolution will relate not so much to competing explanations, but to explanations of different phenomena. Contingency helps us to set out the initial conditions under which evolution occurs, natural selection provides us with the rules governing responses in the evolving populations. The third was that macro-evolutionary patterns will tend to disguise the variability in process that occurs in micro-evolution. By stressing the overall pattern, we have lost sight of the significance of

selective mechanisms as well as the details of the contingent events. Macro-evolutionary approaches cannot be a substitute for looking at the details of micro-evolution.

Gould, in his Introduction, has suggested that the history of evolutionary thought can be represented as a triangle of mechanisms underlying explanations of evolutionary change – adaptation, historicity, and chance. Different schools of thought might place variable emphasis on these, although all would recognize that each must play a role. However, in considering the patterns and processes of hominid evolution, the insight that has emerged most strongly is that these factors are not competitive, but complementary, and that evolution is the outcome of both stochastic and deterministic processes. As such, should the tape of life be replayed, undoubtedly there would be many differences, but there would also be a very significant number of similarities.

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