Adaptive Radiations and Dispersals in Hominin Evolutionary Ecology

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In the context of hominin evolution as a whole, the evolution of modern humans is just a small part of a much larger picture. There has also been increased interest in the later half of the 20th century in looking at human evolution as an adaptive process, involving climatic change, morphological specializations, and behavioral innovations, rather than as phylogenetic history alone. In particular, it is clear that the hominin evolutionary record as a whole shows a series of adaptive radiations. I shall look at the overall pattern of hominin evolution in terms of its constituent adaptive radiations, and what might be the behavioral and ecological elements that underlie each of these.

In the 100 years since the foundation of the Anthropological Institute at Zürich, a spectacular increase in the fossil evidence for human evolution has occurred. In the 1890s, only two extinct hominin taxa were known (*Homo neanderthalensis* and *Homo erectus*), and they were poorly dated and only partially understood. By the end of the twentieth century, well over 2,000 specimens of hominin were known from the Pliocene, and these may be allocated to as many as 23 species (Fig. 1). These discoveries have transformed the study of human evolution. In particular, it is clear that human evolution is neither a continuous and gradual process, nor a single punctuated event. Rather, it is made up of numerous different events, with disparate trends occurring at different rates. In the context of hominin evolution as a whole, the evolution of modern humans is just a small part of a much larger picture. The other major development that characterized the later half of the 20th century has been the increased interest in looking at human evolution as an adaptive process, involving climatic change, morphological specializations, and behavioral innovations, rather than as phylogenetic history alone. In particular, it is clear that the hominin evolutionary record as a whole shows a series of adaptive radiations.[1,2] In this contribution, I shall look at the overall pattern of hominin evolution in terms of its constituent adaptive radiations, and what might be the behavioral and ecological elements that underlie each of these.

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THE PATTERN OF HOMININ EVOLUTION AS A SERIES OF ADAPTIVE RADIATIONS

Figure 2 shows the overall pattern of hominin evolution as revealed by the fossil record, and provides a broad and tentative picture of currently recognized diversity. Needless to say, there is much here that is controversial, in terms of the number of taxa recognized, their time ranges, and their evolutionary relationships.

Time Ranges

The solid bars in Figure 2 show the time ranges of hominin taxa currently recognized or suggested. These are very subject to the vagaries of the fossil record and the availability of dating techniques. Given that all taxa would have geographically localized origins, and that their extinction would also have occurred progressively over a time range, with small populations probably surviving in refugia for some considerable time after the species as a whole has contracted in range, these are likely to be minima.

Phylogeny

The dotted lines in Figure 2 indicate a possible phylogeny for the known hominins, although much of this remains uncertain and hotly debated. In particular, the extent of monophyly among the "robust" australopithecines is questionable;[3] the position of the new find *Australopithecus garhi* has been questioned,[4] and the position of *Homo antecessor* shown here is not that of the authors who proposed the taxon,[5] and its existence has been questioned. Most problematic of all, there is no clear link between *Homo* and *Australopithecus*. Furthermore, the early *Homo* material was recently placed within the australopithecines,[6] and its monophyly is also still uncertain. Within later *Homo*, *H. heidelbergensis* is usu-

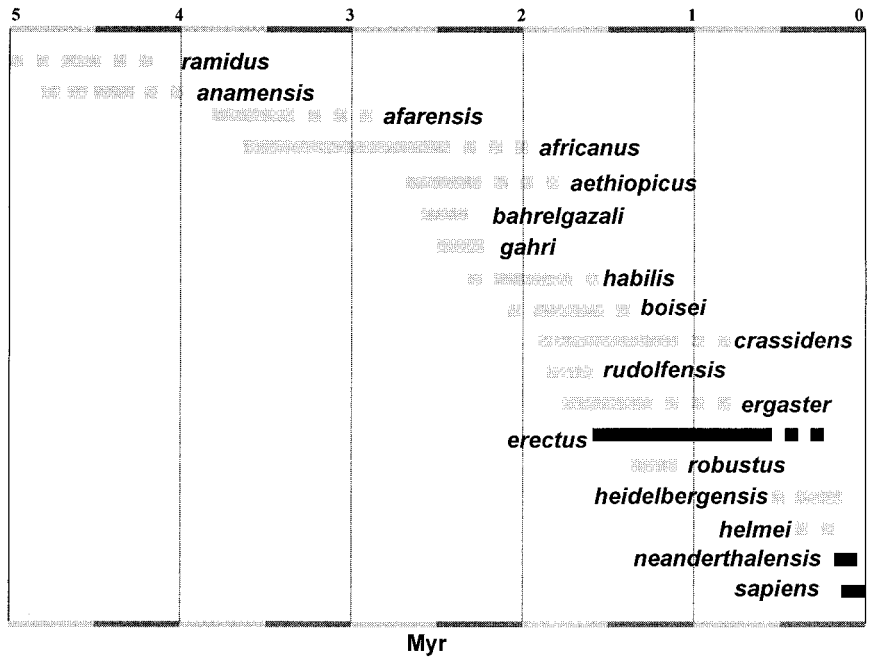

Figure 1. Chronological distribution of the hominin fossil record. Each bar represents a widely recognized taxon. Those shown in black were those known at the end of the nineteenth century, and those in grey by the beginning of the twenty-first.

ally considered to be directly ancestral to *H. neanderthalensis* and *H. sapiens*,[7] but an intermediate species, representing a larger-brained common ancestor (*H. helmei*), was recently proposed.[8] However, despite these caveats, this diagram probably represents reasonably well the emerging picture and scale of hominin evolution. In addition, the late Middle Pleistocene material from East Asia poses further problems which have yet to be resolved.

Species

Probably most controversial of all is the sort of species these "taxa" represent. It is unlikely that they are all biological species in the sense defined by Mayr,[9] and the fossil record is always likely to be intractable to testing this species concept. Most of them can be defined cladistically, in that they possess unique derived traits, but variability and polymorphisms in both ancestral and descendent taxa often make these hard to demonstrate. They are almost certainly species in the sense defined by Simpson (i.e., independently evolving lineages), and thus they map the pattern of hominin evolution well.[10] Howell[11] recently suggested that the term "paleodeme" should be used for all or some of these, as this may reflect better the dynamic and unfixed nature of the evolving populations. At the microevolutionary level at which we should probably be considering hominin evolution, especially its later part, and given the time-transgressive nature of the sample, these are probably a mixture of real biological species and evolving lineages of subspecies. In other words, they could potentially have interbred, but owing to allopatry were unlikely to have had the opportunity. Nonetheless, they provide evidence for independent evolutionary lineages, the genetic isolation of which is beyond the resolution of the fossil record. At one extreme, such as the models preferred by Tattersall,[12] these may be considered species; at another, they may be subsumed within larger groupings. However, from the perspective of evolutionary analysis it is more appropriate to treat them as independent units.[13] It is unlikely that the species concept itself will be the most useful tool for unraveling what is in effect, in comparison with much of the debate about punctuated evolution, a very small-scale event, especially in its later stages (the last half million years).[8]

Superimposed on the taxa in Figure 2 are a series of radiations (grey shading) intended to represent the under-

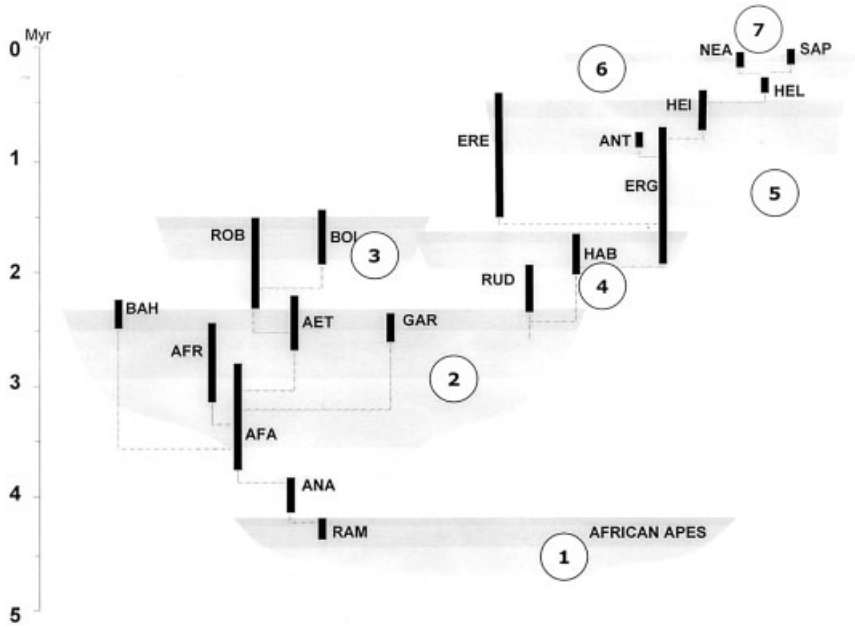

Figure 2. Hominin adaptive radiations. Bars represent lineages recognized in the fossil record, and upturned bells indicate how these may be grouped into adaptive radiations. Numbers indicate adaptive radiations as they are discussed in the text. The monophyletic nature of these radiations remains to be established, but they are identified here by informal taxonomic terms.

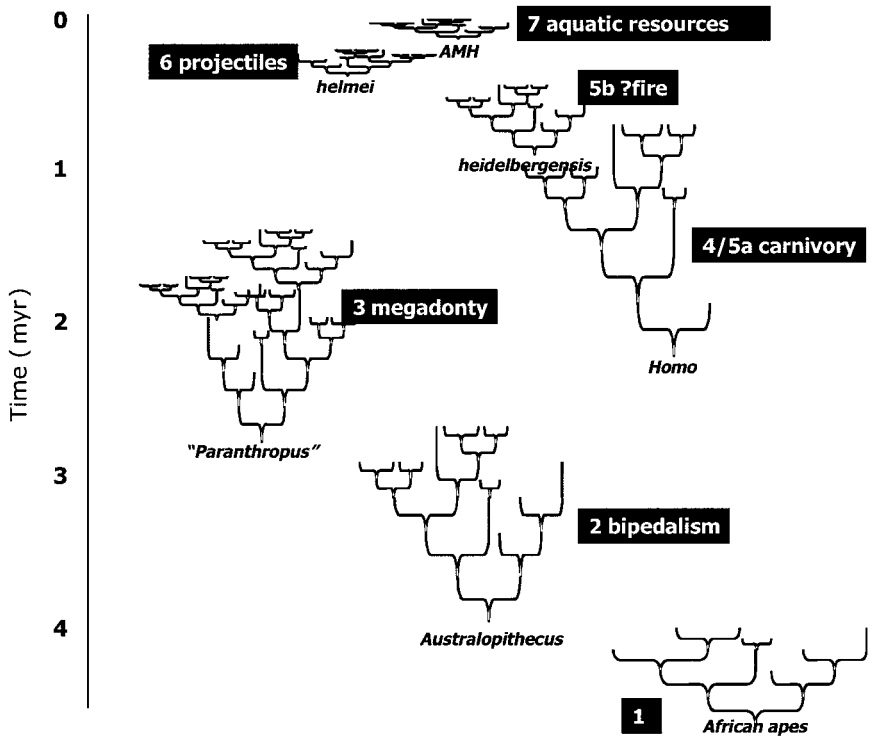

Figure 3. Schematic summary of chronological, phylogenetic, and adaptive pattern of major radiations identifiable in the fossil record. Numbers refer to adaptive radiations identified in Figure 2 and discussed in the text. AMH equals anatomically modern humans.

lying pattern of hominin evolution. It should be recognized that these are abstractions of a continuous process. Broadly speaking, a radiation (adaptive radiation) can be considered to be a dispersal or series of dispersals of descendents of a common ancestral stock (the dispersal being the mark of their evolutionary success), leading to morphologically (and systematically) diverse forms, largely through a process of allopatry and local adaptation and drift. Given the problematic nature of species recognition discussed above, these adaptive radiations should be considered as based more on the process of diversification that arises as a result of dispersals, and the adaptive basis of these dispersals, rather than on the process of speciation as such. In this sense, the term used here may differ in emphasis from that used, for example, to describe the diversification of the mammals as a radiation;[14] there is a substantial difference in scale, but the underlying adaptive and evolutionary process is probably much the same.

The radiations shown here (numbered) are:

1. *The radiation of African apes and earliest hominins in the later Miocene*. This may have been a response to the invasion of Africa from Asia of an ancestral lineage,[15] with the African apes and hominins being the outcome of these dispersals. *Sahelanthropus*, *Orrin*, and the two species of *Ardipithecus* are placed in this radiation very tentatively. The recent discovery of three potential early hominin genera from the Late Miocene and Early Pliocene has shown that this early African ape/hominin radiation may have been more diverse and widespread than previously thought.

2. *The radiation of the bipedal apes (early australopithecines)*. All members of this group, occurring in the Pliocene, have bipedal adaptations, and this seems to be the basis for a widespread, pan-African (Chad, and eastern and southern Africa) series of dispersals. All retain a number of generalized hominin cranial characters, although they also display a trend towards increasing megadonty. The taxa included in this group are *A. anamensis*, *A. afarensis*, *A. africanus*, *A. garhi*, and *A. bahrelghazali*.

3. *The radiation of megadontic specialists* is the dominant trend of the latest Pliocene and early Pleistocene. This seems to be a radiation of more savanna-dwelling hominins, with adaptations towards the processing of coarse fibrous plant material. It is unclear whether this was a monophyletic radiation, or part of a more general series of trends among the australopithecines, all of which show elements of megadonty. Indeed, this may be the trend which characterizes all the early (australopithecine) hominins, and may involve considerable homoplasy. The taxa included in this radiation are *A. aethiopicus*, *A. robustus*, and *A. boisei*.

4. *The radiation of earliest* Homo. This is perhaps the most problematic of all the radiations, as its phylogenetic position is extremely uncertain,[6] and there is considerable variation within the group.[17] *H. rudolfensis* retains megadontic adaptations, while sharing with *H. habilis* an element of brain enlargement. Whether there is more that characterizes this radiation than just a variant on the australopithecine themes of the preceding few million years remains to be seen. The basis for placing it as a radiation lies solely on the fact that it may be a group with a presence in both eastern and southern Africa (SK53, Malawi).[18] It could be arguably placed within later *Homo* or placed among the australopithecines. Furthermore, the new discovery of *Kenyathropus platyops*, which some have linked to *Homo rudolfensis* adds further diversity (and confusion) to this group.

5. *The radiation of* Homo. This, seen in *H. ergaster* and its descendants, may be suggested as a major shift in "grade" or adaptive complex from the australopithecines, shown in cranial and dental morphology, postcranium, behavior, and technology. This radiation may actually be considered two subevents: the first of these is the diversification and dispersal into the warmer parts of Eurasia in excess of 1.0 Myr, and the second is the radiation of later forms (especially *Homo heidelbergensis*) in the period around 0.5 Myr.[7] This second part is more geographically extensive, and in-

cludes the colder temperate parts of Eurasia.

6. *The radiation of larger-brained* Homo. The last half million years or so saw the development of larger-brained hominins, often with very robust morphologies, and associated with the expansion of Acheulean (mode 2) and prepared core (mode 3) technologies, as well as evidence for more human-like behavior. These radiations occur in the context of major glacial-interglacial climatic cycles, and so the underlying biogeographical patterns may have led to repeated dispersals overlain on each other,[8] giving rise to the complexity of the later hominin fossil record: the evolution in Europe of Neanderthals, and in Africa of *H. sapiens*.

7. *The radiation of* H. sapiens. This is a very recent event (last 100 Kyr), and is different from preceding dispersals as it involved far less morphological diversification and resulted in the first complete global colonization.[19]

ECOLOGY AND BEHAVIOR OF HOMININ ADAPTIVE RADIATIONS

The pattern outlined above indicates that, at various points in the course of hominin evolution, a group of hominins was "evolutionarily successful." Such success is indicated by a pattern of geographical expansion, followed by some level of population divergence. Excluding the first of these shown in Figure 2 (that of the African apes as a whole, for which there is no substantial fossil evidence, and therefore no way of linking it to any particular context), it is possible to identify these major points. Broadly speaking, we can think of dispersals/radiations occurring at around 4–3.5 Myr, 2.5–2.0 Myr, 2–1.5 Myr, 0.6–0.4 Myr, 0.3–0.2 Myr, and <0.1 Myr (see Fig. 2). Here, we will consider what might be the evolutionary ecological basis for these events.

Two elements contribute to such events. The first is the environmental context, which may or may not involve an element of change, such as the expansion or contraction of particular habitats. The second is the adaptive novelty that allows for the more extensive or successful exploitation of available habitats. This will certainly involve behavioral innovations, and most probably physiological and anatomical modifications. In effect, there is a geographical basis to all adaptive radiations, in that either habitats to which a species is adapted expand, allowing for dispersal followed by diversification beyond its existing range, or else there is a shift in adaptation which removes barriers to expansion that previously limited the distribution of populations. While it is an oversimplification to view these radiations and dispersals as very discrete events, and to view them as a complete picture of such events, it is perhaps useful to consider what might be the basis for the ones that can currently be inferred from the fossil record.

Early Australopithecines and Bipedalism

There is general consensus that the earliest unequivocal hominins (*A. anamensis* and *A. afarensis*) were bipedal to a considerable extent,[20,21] although they may have also foraged and slept in trees.[22] This would establish bipedalism as a key characteristic of the australopithecine clade, which was established more than 4.0 Myr. Bipedalism provides advantages in the context of reduced tree cover and more open environments, which paleoenvironmental evidence suggests expanded considerably in many parts of Africa during the early and middle Pliocene.[23] Theoretical models suggest that bipedalism conferred advantages in terms of reduced thermoregulatory stress[24] and foraging over larger areas.[25] Bipedalism appears to have provided the basis for hominins to exist across a vast area of Africa by 2.5 Myr: southern Africa, eastern Africa, and across to what is now the eastern part of the Sahel.[26] It is unknown whether they also dispersed into central and western Africa. The accumulating fossil evidence from both eastern and southern Africa suggest that these hominins, while united by a pattern of bipedalism, also exhibited considerable diversity, which may indicate different levels of terrestrial adaptation and ways of exploiting mixed habitats.

"Paranthropines" and Megadonty

From 2.5 Myr until 1.5 Myr, if not later, the primary characteristic that unites most hominins is the enlargement of the molar and premolar tooth rows, and the development of associated cranial and mandibular robusticity associated with heavy chewing musculature.[27] In one sense, this is a continuation of a trend that can be seen among the earlier australopithecines, and there is overlap between early and later forms in the size of the molars. However, the very similar features of both eastern and southern African megadonts suggest that some at least had a monophyletic origin, and were part of a secondary australopithecine (or paranthropine) dispersal. Megadonty has been ascribed to primary dependence upon coarse, fibrous plant foods, perhaps containing high levels of grit.[28] This suggests a more extreme form of terrestrial adaptation, in increasingly open and arid environments, an inference supported by paleoenvironmental evidence.[29] Megadonty may have evolved as a means of maximizing the nutritional return of these early hominins under the relatively arid conditions brought about by climatic change in the later parts of the Pliocene. It allowed hominins (for a million years) to live much as other primates (i.e., on foraged plant resources) in otherwise unavailable habitats.

Homo and Carnivory

Although the origins of *Homo* are obscure phylogenetically, there is little doubt that specimens such as WT15000 indicate a major adaptive shift. This can be seen in the loss of megadontic specializations, the extension of life-history phases, and the enlargement of the brain.[30] There is also some suggestion of either the development of stone tool technology or its elaboration.[31] Perhaps most important of all is the evidence for descendants of this lineage to be found across wide areas of Africa and to have extended to the Caucasus,[32] possibly Pakistan, Southeast Asia, and maybe southern Europe as well.[33] A clue to this expansion of geographical

range is perhaps to be found in the greater evidence for carnivory in the archaeological record.[34] Carnivores by and large have larger geographical ranges and are more habitat-tolerant than herbivores and primates in general.[35] Carnivory, it can be argued, is the basis for this very major adaptive radiation and set of dispersals, and transformed the hominins form a typical primate ape lineage in Africa to a more global one.[1] The shift to carnivory (not full carnivory, but a utilization of meat approaching that found among contemporary tropical hunter-gatherers) represents a change in behavior and ecological strategy, but it is also one that has consequences for gut size, reproductive and growth strategies, and social behavior.

H. heidelbergensis and Fire

Although there is evidence for occasional occupation of the more northerly latitudes of Europe and Asia prior to 1 Myr, it is only after around 0.5 Myr that this becomes more dense and perhaps long-lasting. In Europe at least, this is associated with the appearance of *H. heidelbergensis*, a larger-brained hominin, and also the Acheulean (mode 2 industries).[36] The Acheulean had been present in Africa since prior to 1.0 Myr, but it was clearly not the basis for a more northerly extension. One possibility is that it was fire which enabled the Acheulean toolmakers to colonize more habitats at this point. Evidence for fire older than this date is largely controversial, but the European record after this date does appear to show more substantial evidence for the ability to use fire, and this may account for the timing of these Eurasia dispersals.[33]

H. helmei, Mode 3, and Projectiles

Although disputed, a case can be made on archaeological and palaeontological grounds that there is a further set of dispersals in the period between 300,000–200,000 years across Africa and western parts of Eurasia. The basis for this is the widespread appearance of mode 3 (prepared core) technologies, associated with larger-brained hominins.[8,37] It has been argued that this technology, shared by both later Neanderthals and modern humans, is related to the greater use of projectiles, allowing hunting to take place at a distance from the prey. Stiner et al.[38] argued that there is a shift at about this time in the nature of prey items taken, with a greater cull of highly mobile medium-sized ungulates. Certainly mode 3 technologies, with their greater variety and use of smaller and carefully prepared implements, can be contrasted with the heavy implement/generalized flake production of modes 1 (Oldowan/pebble tool) and 2 (Acheulean), and perhaps indicate a radiation intermediate between those of *H. heidelbergensis* and *H. sapiens*. In terms of environmental components, it is probably the case that the timing of this dispersal, as well as the dispersals associated with *H. heidelbergensis* and *H. sapiens*, is linked to the onset of the glacial-interglacial cycles that became predominant in the Middle Pleistocene.[8]

Homo sapiens and Aquatic Adaptations

The first fossil evidence for *H. sapiens* occurs in isotope stage 6 (ca. 140,000 years ago), and during stages 5, 4, and 3 there is evidence for dispersals out of Africa and across most of the Old World (the New World being colonized most probably after stage 2 (the Last Glacial Maximum). There has been extensive discussion of the adaptive basis for these multiple dispersals, ranging from the origins of language and symbolic thought to the ecological efficiency of the "Upper Paleolithic package."[39–41] However, for the most part these dispersals precede the appearance of the Upper Paleolithic, although elements of them may be present in Africa much earlier.[42] However, one possibility is that the initial spread and success of modern humans is linked to the ability to consistently exploit aquatic resources. Certainly stage 5 shows the first evidence for middens and the effect of human exploitation on shellfish populations.[33] One hypothesis is that the early dispersals of modern humans are a response to this novel behavior, one that provides enormous nutritional advantages.[43] That the first dispersals may have involved coastal adaptations may be a clue to why they show an earlier southern pattern.[33]

CONCLUSIONS

This brief discussion of the adaptive basis for hominin radiations and dispersals is undoubtedly a simplification of a much more complex process, but it does emphasize three key points. The first is that the pattern of hominin evolution is neither a continuous gradual process, with the smooth accretion of human capabilities and features, nor a single spectacular revolutionary event. Rather it is a cumulative process of novel adaptations arising and dispersing in response to climatic and environmental change. The second point emphasized here is that behavioral and ecological elements of adaptations underlie successful dispersals. These in turn are likely to reflect cognitive changes, which led to new ways in which hominins could execute their behaviors and organize themselves socially. A great deal remains to be done to elaborate the links between such behaviors and their underlying cognitive processes. Thirdly, drawing on the general principles of evolution, the model underlying this reconstruction is that dispersals are the key signal of significant evolutionary events, and thus well-documented geographical patterns are the basis for evolutionary ecological analyses in hominin evolution. This in turn requires a good knowledge of the fossil and archaeological record across many areas, and is a reminder of the extent to which paleoanthropology is dependent on chronological and stratigraphic data. The achievements of the twentieth century are due to the extent to which there have been empirical developments, but these have gone hand-in-hand with a growing awareness of the ecological and behavioral basis of the evolutionary process.

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