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Hominid evolution in perspective

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Abstract
The evolution of the Hominidae takes place over some five million years. It involves perhaps as many as a dozen species of hominid, and is in itself a major development by any standards. However, that same period also witnesses a complete revolution in the larger mammal fauna during a time of massive climatic changes, and it is important that our investigations of the Hominidae take sufficient account of the wider perspective. Without such a framework of understanding we risk interpreting every feature of hominid evolution as a special event, separated from the development of life on earth, whereas rates of macro- and micro-evolution among the Hominidae, including speciation, extinction, patterns of dispersion and within-species changes, are better understood as part of that larger whole. This paper gives some examples of evolutionary changes and developments across a range of other mammalian families and attempts to place hominid evolution in a clearer perspective.

Key words: Plio-Pleistocene mammals, climate and evolution, hominid dispersions

Introduction

The Hominidae, in the conventional sense of a family distinct from the Pongidae, has been in existence for something like 5 - 7.5 Ma (Hill & Ward 1988), and has left behind fossil evidence of some dozen species (see Foley 1991) for a convenient summary of views on taxon numbers). From an origin point in Africa, that radiation led to occupation of virtually every landmass via initial dispersions to Eurasia by around 1.0 Ma. The accepted context within which hominid evolution took place has long been recognised as one of massive and to a large extent cyclical climatic change, a backdrop against which we have developed tools and intelligence while consuming many of the species with which we have shared the planet. What is perhaps not so clearly recognised is the larger biotic context of hominid evolution and dispersion within the overall evolution of the mammal fauna. It is only when we take account of the evolution of this larger fauna that we can begin to discern the true evolutionary pattern of the Hominidae, and avoid the dangers of treating every feature of that pattern as a special event that took place in a biological vacuum. Topics such as speciation, extinction and dispersion, in any fossil group, are better examined as part of a much larger whole, where the advantages of data sets spread across several families should overcome the shortcomings of individual treatment or resolution (Turner & Wood 1993a).

I shall begin this discussion of a wider perspective on hominid evolution with a consideration of taxon numbers in other larger terrestrial mammal families from the mid Pliocene to the end of the Lower Pleistocene. Such figures, besides giving us an immediate sense of scale, show just how much potential there is for discerning wider patterns of change.

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Taxon numbers

Archaeologists and physical anthropologists, because of natural divisions in research interest within the subject, are often used to thinking in terms of a relatively small number of hominid species in any one time band. Even treatments that deal with the span of the Plio-Pleistocene tend to confine discussions of hominid evolutionary events and processes to those taxa, without really considering just how small a part of the larger picture this produces. It may surprise many to know that in our current state of knowledge our evolution in eastern Africa between 4.0 and 1.0 Ma involves perhaps seven hominid species in a larger-mammal fauna of 144 species; that in South Africa in the same period only four probable hominid taxa among 83 other species (Table 1). For the 1.0 Ma or so of human presence in Europe (Turner 1992), three possible hominid taxa (the original immigrant plus perhaps *Homo neanderthalensis* and, eventually, *Homo sapiens)* were part of a fauna of 57 larger mammals. If we consider the Plio-Pleistocene as a whole in any major region of the world, then we must conclude that hominids were in the minority.

All of the families listed in Table 1 underwent their own evolutionary developments as a result of the individual evolutionary histories of the constituent species. The numbers of taxa that we have, when seen in the context of the relatively well-understood chronology of many major Plio-Pleistocene deposits, mean that we are in a position to understand a good deal about some of the larger scale patterns of mammalian evolution over the past several millions of years. What should interest us in the present context is the extent to which these developments paralleled those in the Hominidae and thus may be used in efforts to discern the underlying processes of evolution. I shall return to this topic below, but first we need to consider the matter of species and the process of speciation.

Species and speciation

In many respects, the fundamental unit in palaeontology (and neontology) is the species, without attention to which little can be said of the material to hand beyond straightforward description. The species is much more than a convenient pigeon hole for those who deal with the fossil record, since unless we make an effort to deal with the natural divisions of the living world we cannot begin to consider evolutionary trajectories or life histories and integrate palaeontologically-based information with the rest of biology.

Table 1. Numbers of larger mammalian species grouped by family. For East and South Africa, the numbers are for the period between 4.0 and 1.0 Ma. For Europe they cover the period after 1.0 Ma Sources: for East and South Africa, Turner & Wood (1993a) and references therein; for Europe, Turner (1992a) and references therein.

Family	**East Africa**	**South Africa**	**Europe**
Hominidae	7	4	3
Cercopithecidae	16	11	1
Felidae	9	9	6
Hyaenidae	3	7	3
Canidae	2	3	4
Ursidae	-	-	3
Deinotheriidae	1	-	-
Elephantidae	7	1	4
Equidae	11	3	5
Rhinocerotidae	3	2	4
Chalicotheriidae	1	1	-
Suidae	11	4	1
Hippopotamidae	8	1	1
Giraffidae	5	2	-
Camelidae	1	-	-
Cervidae	-	-	10
Bovidae	59	35	14
Total species	**144**	**83**	**57**

Species are most usefully defined genetically in terms of the Recognition Concept as *that most inclusive population of sexually reproducing organisms which share a common fertilization system* (Turner & Paterson 1991). Within the fertilization system are a subset of adaptations referred to as the Specific-mate Recognition System (**SMRS**), which act to bring mating partners together through a signal and response chain (Paterson 1985). The chain may involve chemical, auditory or visual signals, and some of the latter may be visible to the external observer and may even fossilise. Within the normal habitat of the organism the **SMRS** will be under strong stabilising selection, leading to persistence of the species. As a generalised definition based on the idea of what delimits the field for genetic recombination in sexually-reproducing organisms, the Recognition Concept applies equally to hominids. It does so, moreover, notwithstanding the difficulties of applying such a definition to fossils of organisms that do not depend upon largely visual signals for mate recognition (Turner & Chamberlain 1989).

This concept sheds real light on the important question of how speciation takes place. The implications of the Recognition Concept for speciation are that it will be episodic, a cladogenetic event that occurs in small, isolated subsets of a population and is largely driven by changes in external environmental circumstances (Turner & Paterson 1991). Major evolutionary changes, what we recognise as extinctions, speciations and dispersions, should therefore clump together in the fossil record, since environmental shifts sufficient to provoke such changes will be episodic. However, environmental change is necessary but not sufficient for speciation (Vrba 1985: 234), since the propensity to speciate is peculiar to the lineage and dependent on the degree of ecological specialisation. But any responses that do occur should be synchronous across lineages and clades because the motor of change is external to the organisms that make up the groupings.

Since the **SMRS** is strongly habitat specific, it follows that disjunct (allopatric) populations of a species that continue to experience similar habitats will tend to retain the same **SMRS** and will remain members of the same genetic species. This has two important implications. The first runs contrary to the notion that continual gene flow must be invoked to explain the existence of a single species over a wide geographic range. The second is that while allopatry is necessary for speciation to occur in population subsets, it is not a sufficient condition and does not, in itself, inevitably lead to it. Furthermore, since species themselves are not adaptive devices but simply effects of the delimitation of the genetic recombination field, hybridisation between taxa is not something that occurs in defiance of idealised notions of species integrity maintained by natural selection (Paterson 1986: 64). Hybridisation is simply one likely outcome of the co-existence of two populations with sufficient similarities in the **SMRS** components of their fertilization systems, similarities that result from a shared ancestry and that may cover a wide spectrum. It then follows that possible evidence of gene flow in the form of apparent mixing of characters in fossil samples cannot be invoked as a demonstration of conspecificity. Thus the fact that Neanderthals and anatomically modern humans in the Levant may exhibit character mixing (Wolpoff 1989) is in itself no demonstration of conspecificity and no argument against replacement of the Neanderthals by more modern humans from elsewhere (Turner, in press a).

It also follows from the above outline of the Recognition Concept that species have a localised origin, and that the appearance of a new species must then be followed by dispersion into what is later recognised as its range, a point emphasised by Tchernov (1992). It further follows from this that any new species of hominid must also have originated in a single area. This expectation of a localised origin seems to be clearly met in earliest members of the genus *Homo*, and is equally apparent in the distributions of species of *Australopithecus* and *Paranthropus* which appear to have remained confined to regions of eastern and southern Africa (Turner & Wood 1993a: see below). Perhaps more significantly still, in terms of recent concern with the issue of modern human emergence and the question of a dispersion from Africa, it is then apparent that a multi-regional origin of *Homo sapiens* is not a logical option if one believes it to be a new and distinct species.

There is yet one other point to stress when we view species and speciation from this perspec-tive. Much has been made in the past of the ques-tion of species longevity in the fossil record (see, for example, Kurtén 1959a, b), particularly in relation to the probability of extinction with increasing age of a taxon and the search for generalised explanations of turnover based on the concept of evolutionary rates (Van Valen 1973). But if speciation and extinction occur as a result of particular circumstances that bear on the particular fertilization systems of the taxa in question and their response to externally induced changes, then any such rates (or even any apparent correlations

Table 2. Observed effects on various African mammal groups at or after 2.5 Ma. Source Turner Wood (1993a and b) and references therein.

Taxon	**Events at or soon after 2.5 Ma**
Hominidae	*Paranthropus* and *Homo:* hypermasticatory trend: origins of *Homo* and marked diversity
Cercopithecidae	Significant lineage turnover; parallel masticatory developments in *Theropithecus oswaldi*
Carnivora	Incursion of Canis, eventual extinction of machairodonts and continued success of pantherine cats points to effects of change to open country and more cursorial prey.
Deinotheriidae	Gradual extinction
Elephantidae	Very significant increase in hypsodonty, plate numbers and enamel folding in *Elephas recki:*local disappearance of *Loxodonta*
Equidae	Incursion of *Equus*: increased hypsodonty in *Hipparion*
Rhinocerotidae	Increased hypsodonty and grazing adaptations in skull of *Ceratotherium*
Suidae	Increased hypsodonty and tooth volume
Hippopotamidae	Lineage turnover and emphasis on aquatic lifestyle
Giraffidae	No evident change
Camelidae	No evident change
Bovidae	Massive lineage turnover, including immigrations; more open country species; dental adaptations to grazing

between rates in different lineages and clades) ultimately reflect those interactions. In other words, there is no *general* explanation of evolutionary rates other than as the sum of individual reactions, and while there will be similarities in the tempo of speciation for specialist as opposed to non-specialist species - that is taxa more or less closely tied to particular environments and habitats - we can now see that there is no meaningful average of either speciation or extinction rates in any unit of time across lineages and clades as a whole. Any effort to consider hominid species numbers and speciation rates in a wider context must therefore be framed with great caution, so that lifestyle and other clade-specific parameters are fully taken into account.

Climatic change

What then is the evidence for climate as a driving force in the evolution of the Hominidae? The last five million years of the Plio-Pleistocene have been marked by a trend towards lowered temperatures interrupted by a series of stepwise increases in the rate of cooling. This trend has been overlain by the cyclical appearance of glacial and interglacial conditions induced by orbital changes, with the periodic development of massive continental ice sheets and lowered sea levels (Shackleton & Opdyke 1977; Prentice & Denton 1988). The effects of these massive climatic shifts were global in scale: that at 2.5 Ma led to the first major northern hemisphere glaciation (Shackleton *et al.* 1984), to the permanent establishment of the Sahara desert in northern Africa (Van Zinderen Bakker & Mercer 1986) and to the opening up of the eastern African vegetation (Bonnefille *et al.* 1987).

It has been argued that such globally-significant changes in climate, and their effect upon the physical and biotic environment of organisms, are likely to be *the* motor of evolution (Vrba 1985). If that is so, then both macro- and microevolutionary events within lineages and species - events such a speciations, extinctions and dispersions, as well as directional trends within long-lived taxa subject to longer-term selection - should exhibit correlations with environmental changes. (Note. however, that the argument simply proposes correlations for major evolutionary events; it does not dictate the *occurrence* of any particular event in any given lineage at any given time, and brings us back to the point that there is really no larger meaning to averages in species longevity across clades.)

It is at this point that the consideration of hominid evolution necessitates a wider perspective, since it is clear that our framework for assessing the impact of climatic change on evolutionary events must encompass more than just the Hominidae.

Climate and evolution

The climatic event at 2.5 Ma has been singled out here and in several other treatments as one of the most significant in hominid evolution (Vrba 1988; Turner & Wood 1993b). It corresponds broadly with the origin of the robust australopithecine genus *Paranthropus* and, in particular, with the trend towards hypermasticatory development in that lineage. That trend is paralleled to some extent in earliest representatives of the genus *Homo* that appear in the period between 2.5 and 2.0 Ma, since *H. rudolfensis* also exhibits a large mandibular corpus, molarization of the mandibular premolars, enlargement of distal molars, thickened enamel and facial orthognathism (Turner & Wood 1993b).

By itself, such a correlation of hominid developments with climatic events can of course be dismissed, but the effect of the 2.5 Ma event can readily be seen in other African mammals as summarised here in Table 2. Chief among these parallels are the increases in hypsodonty seen in the Elephantidae and Suidae, together with the incursion of *Equus* and marked lineage turnover and changes in dental adaptations in the Bovidae reflecting the increased importance of open country species and dental adaptations to grazing. Looking more widely still, a similar shift to a more open-country fauna is also seen in Europe, together with a longer term pattern of change in faunal composition and evolution within lineages adapting to predominantly colder and more arid conditions (Azzaroli et al. 1988). A similar pattern of change seems to occur in the larger mammalian fauna of the Yushe Basin of Shanxi Province in northern China at around 2.5 Ma (Flynn *et al.* 1991), where extinctions in particular are strongly evident. In other words, neither the origin and subsequent development of *Paranthropus* nor the appearance of *Homo* need be looked upon as isolated evolutionary phenomena. Both are part of a vastly greater transition of the terrestrial mammal fauna at that time, all of which appear to reflect responses to cooling and the opening up of the vegetation. The diversity of precise responses is as great as the diversity of species represented in Table 2, but many appear to be linked to coping with diets of toughened and more abrasive food items.

Dispersions

Hominids originated in Africa, and our own genus appears there sometime prior to 2.0 Ma, perhaps as a result of events connected with the 2.5 Ma climatic shift (Turner & Wood 1993b). As briefly mentioned above, current interpretations of early hominid taxonomy would imply that only with the appearance of *Homo* do we see a change from the more spatially restricted distributions that characterise species of *Australopithecus* and *Paranthropus*, although the later Pliocene large mammal faunas of eastern and southern Africa show evidence of considerable dispersions between the two regions. The first recorded presence of *Homo* in southern Africa appears to postdate its earliest appearance in the eastern region, and may indicate a dispersion of *Homo habilis* into the southern region some time close to 2.0 Ma, although the ear-

Table 3. Latest Pliocene-Pleistocene larger carnivores of Europe and Africa.

Felidae	**Hyaenidae**	**Canidae**
E. Africa: 2.0 Ma		
Homotherium latidens *Megantereon cultridens* *Dinofelis piveteaui* *Panthera leo* *Panthera pardus* *Acinonyx jubatus*	*Crocuta crocuta* *Hyaena hyaena*	*Canis mesomelas* *Lycaon pictus*
E. Africa: after 1.5 Ma		
Panthera leo *Panthera pardus* *Acinonyx jubatus*	*Crocuta crocuta* *Hyaena hyaena*	*Canis mesomelas* *Lycaon pictus*
Europe: 1.0 - 0.5 Ma		
Homotherium latidens *Megantereon cultridens*** *Panthera leo* *Panthera pardus* *Panthera gombaszögensis* *Acinonyx jubatus*	*Crocuta crocuta* *Pachycrocuta brevirostris* *Pachycrocuta perrieri***	*Canis mosbachensis* *Xenocyon lycaonoides* *Cuon alpinus*
Europe: after 0.5 Ma		
Panthera leo *Panthera pardus*	*Crocuta crocuta*	*Canis mosbachensis/lupus* *Cuon alpinus*

** for only part of the time

liest dispersion pattern of *Homo erectus* remains less clear, largely because of continued uncertainties over the taxonomy of the earliest larger members of the genus *Homo* in Africa, those of broadly *H. erectus*-like morphology (Turner & Chamberlain 1989; Turner & Wood 1993a). However, the distributions of African larger mammals, including those of the hominid genera *Australopithecus* and *Homo*, suggest that there is no biogeographical reason to question the monophyletic status of *Paranthropus* (Turner & Wood 1993a).

The appearance of stone tool technology at around 2.4 Ma (Harris 1983; Kibunja *et al.* 1992) in eastern Africa seems likely to be correlated in some measure with these evolutionary developments, reducing ecological constraints (Vrba 1988), increasing the extent to which hominids were capable of modifying their environment and thereby increasing the opportunity for dispersion.

The earliest appearance of *Homo* outside Africa has been widely disputed (Bonifay and Vandermeersch 1991). Levantine sites may prove to contain lithic evidence dating back as far as 2.4 Ma Ronen 1991; Verosub & Tchernov 1991), although the site of 'Ubeidiya is the currently accepted oldest in this region with dates around 1.4 Ma (Tchernov 1992). Elsewhere, the best current candidate is the hominid mandible from Dmanisi in Georgia with a date of around 1.6 Ma based on absolute dating of the underlying volcanic horizon and on the likely age of the fauna (Dzaparidze *et al.* 1992). This find is in a significant position, almost exactly where one might choose to look for evidence of dispersion from Africa, and with a mammalian assemblage containing European later Villafranchian species as well as others linking it to 'Ubeidiya and a strong African indicator in the shape of an ostrich. (It is worth pointing out that the overall similarities of the fauna to that of later, Jaramillo-age assemblages such as Vallonnet and Untermaßfeld in Thuringia have recently been enhanced by the discovery of the machairodont cat *Megantereon* at the latter site. This cat formerly provided some of the strongest faunal evidence for an earlier age of the Dmanisi locality.) However, it is also worth stressing that the Levant contains evidence for later Pliocene movements of mam-malian species into and out of Africa, movements that seemingly became less common during the Pleistocene as a result of progressive tectonic mo-vements and desiccation (Tchernov 1992), so that a Pliocene dispersal of hominids is by no means implausible.

Whatever the timing of earliest dispersion from Africa, it remains abundantly clear that intensive and permanent human occupation of the temperate zones of Eurasia is really a Middle Pleistocene phenomenon, as Isaac (1975) pointed out several years ago. This may appear somewhat paradoxical, since the climatic record shows a swing to more intensive glacial-interglacial oscillations over the last 800,000 years since isotope stage 22 (Prentice & Denton 1988). But when hominid appearance in Europe is considered in the context of habitat and changes to the larger-mammal fauna since the Lower Pleistocene, it becomes apparent that the availability of food resources prior to the Middle Pleistocene is likely to have been highly conditioned by the structure of the guild of larger carnivores (Turner 1992a).

During the glacial periods that came to dominate the past million or so years, Europe was a region of treeless vegetation (Zagwijn 1992: Figure 1) in which animals rather than plant foods would have presented the most consistently available source of food for hominid colonists. In such circumstances scavenging is likely to have been an important means of obtaining food, and successful colonisation would therefore have depended strongly on the structure of the larger carnivore community or guild, members of which would have been in direct competition for available carcases (Turner 1992a, b). Some of the most important changes in this guild occur in the period after 0.5 Ma, at which time it came to bear a strong resemblance to the living guild of eastern Africa (Table 3). I have argued elsewhere (Turner 1992b) that the congruence between this change in guild structure and the increased density of the archaeological and even hominid fossil records suggests a strong causal link, with any earlier hominid immigrants simply unable to obtain sufficiently regular access to carcases in the face of sustained competition from large cats and, in particular, large hyaenas. In other words, the low intensity of hominid occupation during the later Lower Pleistocene implied by the archaeological record can be looked upon as a real pattern with a clearly understandable basis in a wider pattern of evolution within the mammalian fauna.

Such constraints of course imply that localised differences in access to resources may have operated to dictate a regional pattern of hominid distribution. One such area, as I have recently argued, is the Iberian Peninsula, where a seemingly lessened intensity of hyaena activity in particular may have provided more suitable conditions for earliest hominid occupancy (Turner, in press b). For a period in the later Lower Pleistocene there appears to have been no large bone-destroying carnivore in the peninsula until the appearance of *Crocuta crocuta*, perhaps marked by the presence of hyaena coprolites in the latest Lower Pleistocene deposits of Lachar (Aguirre, pers comm; Turner, unpublished data). From the hominid perspective, as potential scavengers, Spain may therefore have offered a more attractive locality than many other parts of Europe during the Lower Pleistocence and the earlier part of the Middle Pleistocene, and might even have offered a refuge until conditions improved in the Middle Pleistocene.

Conclusions

In many senses, the Hominidae may be seen as simply one mammalian family among many, some of whose members happen to have left behind a record of behaviour in the form of artifactual debris. While no sensible investigation of our remote past would ignore that archaeological component, especially since the development of technology must have reduced the constraints of habitat specialisation and contributed in some manner to the subsequent pattern of dispersion, it is clear that the evolution of the Hominidae should be examined within its wider palaeontological context. Once this is done, the role of climatic change in precipitating speciations and evolutionary changes in hominids and other mammals becomes more apparent, as does the interaction between components of the physical and biotic environment in conditioning the suitability of new regions for dispersion and, eventually, permanent occupation.

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