Debating the Environmental Factors in Hominid Evolution

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ABSTRACT

Environmental factors, particularly climatic fluctuations, are widely viewed as important controls on the path of evolution. The broad coincidence of two adaptive transitions in hominid evolution with major climatic milestones supports models in which these evolutionary shifts are climatically driven. In the first, the origin of the Hominidae is tied to the Messinian desiccation of the Mediterranean. A second, more convincing case, involves the origin of the genus Homo and the first appearance of stone-tool technology, which occur in broad contemporaneity with the onset of Northern Hemisphere glaciation in the Pliocene. Detailed analysis, however, encounters difficulties in tying large-scale forcing phenomena to the terrestrial evidence for hominid evolution, and in resolving the effects of interacting environmental factors. The influences of climate, tectonics, volcanism, and community evolution all act at varying scales, and are reflected in different ways in the geologic record. Current research is tying detailed studies from the African continent to records of global change, and to better understanding of the interactive effects of various environmental factors with human evolution.

INTRODUCTION

The prospect of global-scale environmental change is currently driving an intensive interdisciplinary research effort on the effects of wide-ranging processes including climatic forcing, tectonics, volcanism, and community evolution. How these and other factors will affect the future of humankind is one of the great mysteries in scientific research today. Just as the future of our species will depend upon responses to environmental factors, our past is marked by a long record of adaptation to environmental conditions and change. As details of our evolutionary past emerge from the fossil record, related investigations are forging a picture of the environmental context through which we evolved, and raising questions on the nature of adaptive responses to a dynamic Pliocene-Pleistocene environment.

Paleoanthropology has long suffered from a paucity of evidence detailing both the array of hominid lineages and the world in which they evolved. But discoveries over the past several decades have greatly expanded the direct fossil evidence of our family, the Hominidae, and a focus on interdisciplinary investigations has strengthened the basis for assigning ages and reconstructing the communities and ecosystems in which they developed. In parallel with these advances has been an explosion in data on global-scale phenomena through the later Cenozoic, and particularly on the evolution of Pliocene-Pleistocene climate and tectonic history. Now, hard questions of cause and effect are being posed, as scientists try to relate the major adaptive shifts in our lineage to global environmental change at the end of the Miocene.
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Memorial Preprints

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environmental controls and episodes of change.

Paleoanthropology is still very much a discovery-driven science. Thus, each new fossil can greatly augment the available evidence and alter perceptions of hominid ancestry (e.g., Kimbel et al., 1996). In contrast, the data relating to geological context and the environmental setting for hominid evolution is extensive and diverse, with new discussions and publications appearing regularly. Most recently, a lengthy compilation of papers on climate and hominid evolution has been published (Vrba et al., 1995), a conference in Malawi sponsored by the Wenner-Gren Foundation addressed questions of biogeography and evolutionary theory as they relate to hominids (Sikes and Wood, 1996), and the 1996 GSA Annual Meeting in Denver hosted a debate on the climatic control of hominid evolution. Environmental influences and the driving forces behind hominid evolution have also been examined in the popular literature (Stanley, 1996; Potts, 1996a). As more and more data accumulate, there has been a trend away from simplistic, single-cause scenarios, and toward a more integrative approach to environmental factors. The result is a more balanced assessment of problems and an increasingly geological perspective to some major questions in hominid evolution.

RADIATIONS OF THE HOMINIDS

Although there are many difficult questions remaining in the reconstruction of a phylogeny for the hominid family, the main features of that story are now becoming clearer. There are two primary adaptive transitions in the hominid record: a shift to a full upright bipedal mode of locomotion (which characterizes the family), and a dramatic increase in the size of the brain (associated with the genus Homo; Fig. 1).

The record of bipedalism in the Hominidae is most graphically preserved in the fossil trackways at Laetoli, Tanzania (Fig. 2), where the 3.6 Ma footprints of three individuals were uncovered by Mary Leakey’s excavations in 1978–1979 (Leakey and Hay, 1979). Fossil specimens...
from Laetoli are attributed to the taxon *Australopithecus afarensis*, which is also well represented in the collections from Hadar in Ethiopia, ranging down to near 3 Ma (Johanson et al., 1978; Kimbel et al., 1994). The record of hominin bipedalism can be extended back to 4.2 Ma (Leakey et al., 1995; see Fig. 3). At that time another species, *Australopithecus anamensis*, already had features suggestive of specialized bipedal locomotory abilities. The development of hominin bipedalism was thus an adaptation that occurred even earlier than *A. anamensis*. The sparse fossil record prior to 4.2 Ma, however, leaves the timing and context of this transition uncertain.

The second major adaptation in the hominid lineage, and the one that sets our line apart from the australopithecines, is an increased cranial size relative to body size. This trait is already established in the oldest securely dated cranial specimens of the genus *Homo* at 1.9 Ma, and thus likely entered the hominid repertoire of adaptations in the 2–3 Ma interval. The oldest specimen attributed to the genus *Homo* is the 2.4 Ma maxilla recently reported from Hadar, Ethiopia (Kimbel et al., 1996). Possibly associated with the increase in brain size is the adoption of stone-tool technology as a behavioral adaptation; its earliest record is at 2.5 Ma (Semaw et al., 1997). Within the genus *Homo*, there is a dramatic radiation of species at about 1.9 Ma. At least three species are present in the record close to this time, *Homo habilis*, *H. rudolfensis*, and *H. erectus* (see Fig. 3). On the basis of the available material, it is difficult to assign earlier material to species.

Parallel to the diversification of the *Homo* lineage is a radiation that includes a gracile hominin, *Australopithecus africanus* appearing between 2 and 3 Ma, along with a robust form, *Paranthropus aethiopicus*. The robust lineage is represented by two further species, *P. boisei* and *P. robustus* in the interval between 2 and 1 Ma.

The origins of bipedalism remain poorly understood, as few fossils or localities of the appropriate age are currently known. The origin of the genus *Homo*, however, and the radiations in both the *Homo* and *Australopithecus* lineages occurred in times that are well represented in the geologic record of Africa, and both fossil evidence and details of context are abundant.

**GLOBAL CLIMATIC CHANGE**

Nearly every discussion of hominin evolution includes a link to global change. While there is no question that important global climatic changes were underway through Pliocene-Pleistocene time, it is less clear that (1) individual “events” can be identified in the global record or in the records associated with hominin fossils, (2) that climatic effects were sufficiently strong to affect low-latitude Africa, particularly those parts inhabited by hominids, or (3) that climatic effects can be uniquely implicated among interacting environmental factors.

Connections between global climate, particularly temperature-precipitation shifts, and steps in hominin evolution have long been used to explain the major adaptive shifts recognized in our ancestry (e.g., Brain, 1981; Laporte and Zihlman, 1983). For example, the origin of the Hominidae is often related to drying in the Messinian, and the splitting off of the *Homo* branch to the onset of Northern Hemisphere glaciation. As already noted, there is currently insufficient evidence to evaluate the Messinian-hominid connection, but they do appear to be broadly contemporaneous. More can be argued about the connection between Northern Hemisphere glaciation and the origin of *Homo*. The influential paper by Shackleton et al. (1984) aroused tremendous interest in the paleoanthropological community, placing the onset of major Northern Hemisphere glaciation at 2.4 Ma. This corresponded well to theoretical perceptions for the record of *Homo*, but until recently there has been little fossil evidence to support such an antiquity for the genus. The existence of stone tools in the record back to 2.4 Ma, however, was taken by many to be trace-fossil evidence for *Homo* of that age. It is important to note that very little of adaptive significance is known about earliest *Homo*; thus, arguments relating to this evolutionary event are highly speculative. What is known is that this event probably occurred in the interval between 2.5 and 3 Ma, and is thus roughly coincident with important high-latitude events marking the development of Northern Hemisphere glaciation. This makes it fair

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game for consideration as a consequence of climatic forcing.

A recent summary of the climatic argument for hominid evolution is deMenocal’s (1995) synthesis of evidence from the marine realm which shows convincingly that the dramatic oscillations driven by orbital periodicities, which characterize the high-latitude record of the Pliocene-Pleistocene, were clearly felt in low-latitude Africa. He analyzed marine dust records off both the east and west coasts of Africa, and combined this data set with oxygen isotope results (Fig. 3) to show both long-term trends and variations in frequency of climatic oscillations. Four features of this data set are significant here. There is a long-term trend over the past 4 m.y., marked by increasing dust and heavier $\delta^{18}O$ values, documenting a shift toward cooler and drier conditions. Oscillations in both data sets reflect changing dominance in orbital parameters, from a precessional (23–19 ka) mode prior to 2.8 Ma, to an obliquity (41 ka) pattern between 2.8 and 1 Ma, and finally to an eccentricity-dominated (100 ka) periodicity after 1 Ma. The dust record provides direct evidence that these global climatic oscillations affected terrestrial ecosystems in at least the northern part of low-latitude Africa. Although the timing of shifts in dominant periodicity can be quantified, it is unclear whether these represent the sort of “events” sufficient to trigger evolutionary response in terrestrial communities.

Two other questions remain to be answered. The first concerns how much of the continent provided the signal recorded in the marine dust records. Present-day dust flux off Africa is derived primarily from already arid regions around the Sahara, and Holocene variations have been attributed to shifts in the extent of that arid belt. The signals recorded in the marine dust record do not necessarily imply threshold changes in wetter habitats on the continent, and thus may not have directly affected organisms there. The impact of periodicities and their shifts must be directly measured in the environmental record of individual sites and basins associated with the record of hominid evolution in order to establish that link. The second question concerns the ability to discriminate among various interacting environmental factors and to uniquely identify climatic signals. While the large-scale response across northern Africa recorded by deMenocal (1995) calls for large-scale controls such as climate, when we begin evaluating the record directly associated with hominid evolution, more local- and regional-scale phenomena may obscure such signals. It is also important to consider that global climate in the Pliocene-Pleistocene

Figure 4. Fossiliferous sediments like this fluvial channel and overbank couplet at Koobi Fora in the Turkana Basin have yielded a detailed record of steps in hominid evolution and the environmental context in which it took place.

was affected not only by orbital factors, but also by tectonic developments and changes in oceanic circulation, other very large-scale phenomena. The Pliocene-Pleistocene ice ages were ultimately driven by major tectonic events including the uplift of the Tibetan Plateau and the closing of the Isthmus of Panama (Stanley, 1995, 1996; Stanley and Ruddiman, 1995).

COMPETING HYPOTHESES

Most hypotheses put forth to explain patterns in evolution include environmental inferences in either an active or passive role. Three hypotheses that have been proposed to relate the evolutionary record of the Hominidae to climatic fluctuations are: (1) the long-held “savanna hypothesis,” in which a relative shift toward cooler and drier conditions causes a change from more forested to more open vegetation; (2) the “turnover-pulse hypothesis” (Vrba, 1996a), with more specific conditions and implications; this relates broad-based faunal turnovers to environmental (here specifically climatic) events; and (3) the “variability selection hypothesis” (Potts, 1996a, 1996b), focusing not on individual events or shifts, but rather on the repetitive nature of environmental oscillations through time. Each of these has its adherents, and its strengths, as discussed below.

Lurking in the background of discussions on hominid evolution for decades has been the savanna hypothesis. Although commonly invoked (e.g., Klein, 1989), it does not seem to have been explicitly stated or clearly defined. As a basis for reference, the idea has been summarized recently by Potts (1996a). In this hypothesis, cooling and drying leads to a decrease in forests and a spread of grasslands, in either a gradual or abrupt fashion. The idea’s beauty is in its simplicity, and it has been applied to explain a wide range of evolutionary trends, from the origin of the Hominidae to the origin of the genus Homo, and other events as well.

The turnover-pulse hypothesis attempts to link temporally restricted clusters of speciation and extinction events with climatic shifts. In a sense, it uses the same process as the savanna hypothesis, but applies it in two directions (that is, cooler and drier trends or warmer and wetter trends) and over varying scales. As applied to the record of hominid evolution, it has become the focus of interest in tying a climatic “event” associated with the onset of Northern Hemisphere glaciation to the appearance of Homo and of stone tools (Vrba, 1996b; Semaw et al., 1997). The two difficulties in testing this hypothesis center on how an “event” is defined and on the treatment of data showing significant levels of speciation and extinction (see below). Other workers, including Prothero (1995), have argued that as a generalization the hypothesis does not work. In test cases in the early Cenozoic, prominent climatic signals do not herald major speciation or extinction events among mammals.

The most recent addition to the field is the variability selection hypothesis of Potts (1996a, 1996b). This relates speciation to repeated shifts in selection over time, as environmental oscillations are reflected in fluctuations of landscape characteristics. The variability hypothesis focuses on the overall pattern of changes
adapted taxa. There are methodological differences between the two studies, particularly with respect to the treatment of rare taxa. Vrba (1996b) emphasized the significance of rare forms, often known from only a single specimen, as they demonstrate the presence of immigrant forms predicted in the turnover-pulse hypothesis. But the rarity of these taxa makes it impossible to evaluate whether an occurrence represents a first appearance (as an immigrant) or simply an artifact of collecting or taphonomic biases against rare forms that were, however, present earlier. It is also possible that the faunal transition recorded for 2–3 Ma occurred as several pulses, which may even have differed in relative magnitudes. This argument highlights one side of the problem in linking evolution and environment, that of discerning the character of evolutionary patterns from fossils.

Beyond these problems of interpreting the mammalian data looms a more intractable problem of separating the effects of multiple environmental factors acting on an ecosystem. Geological investigations in the Turkana Basin have led us to recognize a diverse array of environmental factors, acting over different time periods and with different intensities (Feibel, 1995). Because of its large size and predominantly fluvial nature, the Turkana Basin is influenced by two climatic regimes: a relatively wet seasonal regime in its Ethiopian Highlands catchment area, and a semiarid seasonal regime in the lower elevation depositional basin. At present, these regimes are out of phase, such that the rainy season in the catchment occurs during the dominant dry season of the lower basin. Similarly, two aspects of volcanism affected the basin in the past: occasional proximal events in the form of lava flows, and more common influxes of tephra from distal sources in the Ethiopian Highlands. Tectonics also played a major role in complicating the environmental picture, with a history of uplift and subsidence on a series of alternating half graben and marginal blocks. Interdependent upon these factors were changes in landscapes related to depositional settings, vegetation patterns, and soil development which also propelled change in the basin's commodities.

Geologic evidence commonly points out which of these factors are dominant at a given time—for example, an influx of volcanic ash is quite conspicuous—but it is more difficult to evaluate the interactions among these factors. A high sedimentation rate due to volcanism can cancel out the effects of increased subsidence, but climatic interactions are more difficult to assess. There are now numerous examples in which a dominant factor obscures our perspective of what's happening with another. A case in point is the Omo micromammal record.

Micromammals are generally regarded as excellent indicators of local habitat and environmental conditions. In a study of such faunas from the northern part of the Turkana Basin, in the Omo Valley, Wesselsman (1984, 1995) documented a dramatic local change from primarily mesic (requiring moderate amounts of water) to dominantly xeric (low water need) forms. He interpreted this purely in terms of a climatically driven system, using his evidence to support a climatic shift at ca. 2.5 Ma. Geologic evidence, however, points to other possible causes for the observed patterns. Beginning around 2.5 Ma, the Stephanie uplift, a basement-cored structural block that now borders Lake Stephanie (Chew Bahir) in Ethiopia, began to develop. This uplift shed coarse volcanic detritus off its southern margins, and coarse metamorphic debris farther north. This metamorphic debris entered the Omo sedimentary record at this time, and became the raw material utilized in early stone-tool manufacturing (Merrick, 1976; Howell et al., 1987). These sediments display a shift from a large meandering river to a shallow braided system. What this likely represents is a displacement of the axial, meandering river by a clastic wedge of basin-margin alluvium. The axial system was a large perennial river fed by the highlands catchment, and the marginal system was composed of short ephemeral streams draining the arid local margin (Feibel et al., 1991). The shift in character of the micromammal assemblages could thus be explained simply as a product of tectonic activity and sedimentary response, or as a product of tectonics and other factors. But in this case, what is certain is the tectonic effect; the contribution of climate here remains unclear.

Similar arguments can be made for the influence of explosive volcanism and the influx of voluminous tephra into the sedimentary basin. These events have the ability to transform the landscape, and to rearrange floral and faunal communities, effects that mimic climatic signatures. The record of tephra influx into the basin is cyclical; three cycles are recorded, spanning 4.2–3.4 Ma, 3.4–2.5 Ma, and 2.5–1.6 Ma. Each increased in intensity through time, and subsequent cycles exceeded the magnitude of precursors. Although single eruptions were no doubt dramatic, their individual effects seem to have been short-term. However, the cumulative effects at the peaks in eruptive cycles were enough to disrupt depositional systems and dramatically alter the pattern of communities across the landscape (Rogers et al., 1994). This effect is most clearly seen around 1.6 Ma, but the coincidence of the 2.5 Ma activity peak with global climatic shifts implies that whatever signal we find in

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The common theme that unites nearly all of the studies on the context of hominid evolution is the complex mix of often conflicting environmental signals. There are two aspects of scale involved here: spatial scales of variability in terrestrial systems, which may vary dramatically on a scale of meters to tens of meters, and temporal scales of sampling, where data may represent fossils accumulated over a few years or a suite of assemblages representing hundreds of thousands or even millions of years. These data must somehow be integrated with a regional and global data set that records effects on many different scales.

The adjective often employed for habitats of Pliocene-Pleistocene terrestrial systems in Africa is “mosaic,” in which complex ecotones separate forest, woodland, bushland, and grassland in a landscape not only spatially heterogeneous, but also temporally dynamic. Such complexity is probably the norm in terrestrial ecosystems through much of time, and it cannot be ignored in attempting to tie together the adaptive responses occurring on a dynamic landscape and the interacting environmental signals that mold that system.

The major adaptations that molded the hominid lineage took place in Africa within a context of environmental change: climatic swings, tectonic upheaval, volcanism, and evolving faunal and floral communities. As new discoveries of fossil remains resolve details along the hominid trajectory, far-ranging investigations of environmental characteristics raise questions of both the context and the driving forces behind this evolutionary story. While the global pattern of climate change through the Pliocene-Pleistocene is well documented from high-latitude settings, it is unclear how directly Pleistocene is well documented from high-latitude settings, it is unclear how directly the driving forces behind this evolution—raise questions of both the context and investigations of environmental characteristics upheaval, volcanism, and evolving faunal environments of Pliocene-Pleistocene terrestrial systems in Africa through much of time, and it cannot be ignored in attempting to tie together the adaptive responses occurring on a dynamic landscape and the interacting environmental signals that mold that system.

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Building Knowledge for a Nation of Learners: A Framework for Education Research

“Building Knowledge for a Nation of Learners” marks the Department of Energy’s “first attempt to develop a single comprehensive vision of the nation’s future needs for knowledge about education, and to set clear priorities for educational research geared to meeting those needs.”

Early this year, the Department of Energy released a new National Priorities Plan entitled “Building Knowledge for a Nation of Learners: A Framework for Education Research.” The report, the first in a new series of biennial reports, establishes national priorities for education research. These priorities are based on a recognition that the nation is strengthened by a population that values and pursues a lifetime of learning, and that a critical prerequisite for meeting this goal is an investment in education research to improve the achievement of all learners. The report presents an education research agenda for the 21st century. It is meant to serve as an agenda for supporting the development of knowledge about how to improve teaching and learning in the nation’s schools.

More than 500 parents, teachers, education researchers, and representatives of business and community organizations were consulted in preparing the agenda, which was developed by the department’s Office of Educational Research and Improvement and a 15-member National Educational Research Policy and Priorities Board, co-chaired by Southern Illinois University president and former Education Under-Secretary Ted Sanders and Stanford University education professor Kenji Hakuta.

As defined by the report, the National Priorities for Research in Education are:

1. Improving learning and development in early childhood so that all children can enter kindergarten prepared to learn and succeed in elementary and secondary schools;
2. Improving curriculum, instruction, assessment, and student learning at all levels of education to promote high academic achievement, problem-solving abilities, creativity, and the motivation for further learning;
3. Ensuring effective teaching by expanding the supply of potential teachers, improving teacher preparation, and promoting career-long professional development at all levels of education;
4. Strengthening schools, particularly middle and high schools, as institutions capable of engaging young people as active and responsible learners;
5. Supporting schools to effectively prepare diverse populations to meet high standards for knowledge, skills, and productivity, and to participate fully in American economic, cultural, social, and civic life;
6. Promoting learning in informal and formal settings, and building connections that cause out-of-school experiences to contribute to in-school achievement;
7. Understanding the changing requirements for adult competence in civic, work, and social contexts and how these requirements affect learning and the futures of individuals in the nation.

The priorities are focused on early childhood learning, student learning, effective teaching, strengthening schools, student diversity, learning beyond the classroom, and adult competence.

The report includes the chapter “Putting the Priorities to Work,” which challenges Americans from all walks of life to get involved in the process of educational improvement and to take greater responsibility for results. State and local decision-makers and educators can get more involved by accessing and using the research through a nationwide system of regional education laboratories, national research and development centers, and clearinghouses. Other sections include “An Open Letter to the American People” and a prologue, “What Do We Need to Know?”

Because public participation is invited, the earth science community may wish to closely follow this process to see that our discipline is included in the evolving agenda and to provide input so that our nation’s educated citizens of the 21st century are earth science literate.

The report is available in DOE’s “Online Library” Web site at http://www.ed.gov/offices/OERI/RschPriority/plan/.

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