

2. Environmental hypotheses of Pliocene human evolution

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Abstract

Substantial evolutionary change in Pliocene hominins affected a suite of behaviors and anatomical features related to mobility, foraging, and diet – all related to the ways in which hominins interacted with their biotic and physical surroundings. The influence of environment on evolutionary change can be stated as a series of hypotheses. Adaptation hypotheses include the following: novel adaptations emerged in hominins and contemporaneous mammals (1) within relatively stable habitats; (2) during progressive shifts from one habitat type to another; and (3) due to significant rises in environmental variability. These ideas further suggest the “adaptability hypothesis”: (4) since adaptations potentially evolved in environmentally stable, progressively changing, or highly variable periods, lineages have differed in their ability to endure environmental fluctuation. Thus, extinction of certain adaptations (and lineages) should have corresponded with heightened environmental variability, while new adaptations evolved during those periods should have enabled a lineage to persist (and spread) through a novel range of habitats. Turnover hypotheses, on the other hand, concern the timing and processes of species origination and extinction in multiple clades. These hypotheses state that species turnover; (5) was concentrated in a narrow interval of time related to a major climate shift; (6) spanned several hundred thousand years of climate change, and occurred in a predictable manner dependent on the nature of species adaptations; and (7) took place gradually over a long period as lineages originated, persisted, or went extinct within a changing mosaic of habitats. A separate, biogeographic hypothesis regarding faunal change posits that; (8) substantial climatic and tectonic disruptions resulted in multiple episodes of faunal community formation (assembly) and breakup (disassembly). This assembly–disassembly process may have had profound effects on Pliocene and Pleistocene faunas of Africa and on researchers’ ability to infer significant events of faunal evolution from fossil sequences at the basin or sub-basin scale. Since all ideas about environmental effects on evolution depend on temporal correlation, an important challenge is to match faunal sampling to the precessional (~20 Kyr) and obliquity (41 Kyr) scale of Pliocene climate dynamics.

Key Events in Pliocene Human Evolution

This chapter describes the range of hypotheses that relate early human evolution and environmental change in the Pliocene. Age-calibrated data sets now tell us a lot about

African Pliocene environmental dynamics. Yet this information becomes relevant to questions of human origins only if we can identify what the pivotal events of hominin evolution were and when precisely they occurred. Likewise, evaluating how environmental change shaped

mammalian faunas relies on defining the precise timing and nature of species turnover and adaptive evolutionary shifts. One reason mammalian faunas are such a compelling area of inquiry is that fossil mammals comprised part of the early hominin environment, and they involved taxa whose phylogenetic, adaptive, and biogeographic trajectories were shaped as much, or as little, by environmental factors as early hominins'. The aim here, then, is to dissect the ways in which environmental change and human evolution may have coincided, with an eye on the broader question of how environmental conditions affected East African mammalian fauna. We begin here with a short list – a proposal of the main events in Pliocene human evolution.

SPECIES ORIGINATION AND EXTINCTIONS

The oldest hominins may be late Miocene in age, with the relevant fossils from Chad, Kenya, and Ethiopia assigned to three genera – *Sahelanthropus*, *Orrorin*, and *Ardipithecus* (Haile-Selassie, 2001; Senut et al., 2001; Brunet et al., 2002; Haile-Selassie et al., 2004). The record is, at present, too incomplete to know whether the temporal range of *Sahelanthropus* or *Orrorin* extended into the Pliocene, if indeed either lineage had significant longevity. Although little is known about *Ardipithecus kadabba* (roughly 5.8 to 5.2 Ma [Haile-Selassie, 2001]), the first appearance of *Ar. ramidus* at ~4.4 Ma at Aramis, Ethiopia, implies a species origination in the early Pliocene (White et al., 1994, 1995; Renne et al., 1999). Fossils from the site of As Duma at Gona, Ethiopia, have also been attributed to *Ar. ramidus* (Semaw et al., 2005); but since these fossils, dated between 4.51 and 4.32 Ma, are chronologically indistinguishable from those of Aramis, the origination and extinction times of *Ar. ramidus* are still poorly constrained. It is an important point that when the first appearance datum

(FAD) and last appearance datum (LAD) of a taxon are essentially the same, its “lineage history” and possible environmental influences on its origination and extinction are virtually impossible to evaluate.

The genus *Australopithecus* originated during the early Pliocene based on the first appearance of *Au. anamensis* in the Turkana basin at ~4.1 Ma (Leakey et al., 1995, 1998). The FAD of *Au. afarensis* at ~3.6 Ma (Laetoli, Tanzania) – or possibly as early as ~3.85–3.89 Ma (Belohdelie, Ethiopia; [Asfaw, 1987; Renne et al., 1999]) – and its LAD at ~2.95 Ma (Hadar, Ethiopia), would appear to reflect significant evolutionary events (Leakey and Harris, 1987; Lockwood et al., 2000; White et al., 2000). *Au. afarensis* is currently one of the best-defined and best-calibrated lineages of Pliocene hominins, and shows evidence of evolutionary change late in its currently known time range (Lockwood et al., 2000).

Au. africanus's first appearance, in South Africa, is less well calibrated, placed conservatively at ~2.8 Ma (Makapansgat), and possibly back to ~3.3 Ma (if the “little foot” skeleton, STW 573, from Sterkfontein Mbr 2 represents this species) (Vrba, 1995b; Clarke, 1999). The lineage persisted for at least 300 Kyr, possibly closer to 1 Myr, if the faunal age estimate of ~2.5 Ma typically linked to the *Au. africanus* sample from Sterkfontein Mbr 4 is correct (Vrba, 1988).

A fossil of *Australopithecus* (*Au. bahrelghazali*) from Chad, assigned to ~3.5 Ma (Brunet et al., 1995), shows similarities to *Au. afarensis* and raises the question of biogeographic exchange across distant regions of Africa during the Pliocene (Strait and Wood, 1999). The timings of such exchanges are difficult to pin down. The likelihood that *Australopithecus* is paraphyletic creates further uncertainty about the diversity of Pliocene hominins (Skelton and McHenry, 1992; Strait et al., 1997; Strait and Grine, 2004).

It is partly due to the parphyly of *Australopithecus* that the new genus and species

Kenyanthropus platyops was named, based on an assemblage of fossils from Lomekwi in the Turkana basin, including a single, poorly preserved cranium (Leakey et al., 2001; see also White, 2003). Whether this fossil assemblage at ~3.5 Ma represents its own evolving lineage or a short-lived variation best joined with other fossils currently assigned to *Australopithecus* is not yet certain.

Two other significant Pliocene evolutionary events include, first, the origination of *Paranthropus*, based on a FAD at ~2.7 Ma (represented by L55s-33 mandibular fragment from Omo sub-Member C6) – i.e., a lineage sometimes called *P. aethiopicus* (best represented by WT-17000 cranium from West Turkana at ~2.5 Ma) – and, second, a likely phyletic transition from *P. aethiopicus* to *P. boisei* at ~2.3 Ma (Suwa et al., 1996). Although cladistic analysis supports “robust australopith” monophyly (e.g., Strait et al., 1997), the possibility of deriving *P. robustus* from *Au. africanus* in southern Africa (e.g., Rak, 1983) would require taxonomic revisions and an addition to our list of late Pliocene speciation events. Further evidence of megadontia comes from *Au. garhi*, based on fossils from Bouri, Ethiopia, at ~2.5 Ma (Asfaw et al., 1999), but it is uncertain whether this specific name refers to a sustained lineage or a short-lived variant of *Australopithecus*.

Timing of the origin of *Homo* depends on the criteria used to define the genus. Candidates believed to signal that epic event include: (1) the hypothetical coincidence of earliest *Homo* with stone toolmaking (e.g., Leakey et al., 1964), with the FAD for stone tools currently at ~2.6 Ma (Semaw et al., 2003); (2) the appearance of molars similar to those of *H. rudolfensis* in the Omo sequence at ~2.4 Ma (Suwa et al., 1996); (3) the Chemeron temporal bone fragment at ~2.4 Ma (Hill et al., 1992); (4) the AL-666 maxilla attributed to *Homo* at ~2.3 Ma (Kimbel et al., 1997); (5) neurocranial enlargement by about 1.9 Ma, indicated by crania KNM-ER 1470 and ER

1590 in the Turkana basin; (6) the appearance of African *H. erectus/ergaster* possibly by 1.9 Ma, indicated by occipital fragment KNM-ER 2598 (Wood, 1991); or (7) a reconfiguration of body proportions and size (Wood and Collard, 1999) by about 1.7 Ma (Ruff and Walker, 1993), though perhaps by ~1.9 Ma, as indicated by the large innominate KNM-ER 3228 in the Upper Burgi Member at Koobi Fora, and by reanalysis of femur length in *H. habilis* (Haeusler and McHenry, 2004).

In assessing faunal or other environmental events associated with the origin of *Homo*, therefore, it is essential to indicate exactly which earliest marker of the genus is adopted and why.

EXPERIMENTATION IN DENTAL PROPORTIONS

One or more instances of divergence between megadont and smaller-toothed lineages took place during the Pliocene (Grine, 1988; Wood, 1991; Suwa et al., 1994; Teaford and Ungar, 2000). Greater postcanine tooth size is coincident with the origin of *Paranthropus*, and increased megadontia apparently occurred as a trend in this genus over time, although the rate and steadiness of molar and premolar size increase are not altogether clear. Megadontia in Pliocene hominins is generally correlated with cranial evidence of hypermastication, including substantial cresting along the insertions of chewing muscles and architectural modifications (e.g., substantial anterior pillars, facial “dishing”) related to high-chewing forces (Rak, 1983; McCollum, 1999). The presence of prominent anterior pillars in *A. africanus* implies, however, that at least this architectural feature is not always associated with hypermastication and strong megadontia.

Smaller postcanine dentitions are typically assigned to early *Homo sensu lato*; yet megadont dentition may sometimes have been coupled with neurocranial enlargement (e.g., KNM-ER 1470)

possibly indicative of *Homo*. While megadont dentition is often coupled with small canines and incisors, evidence of hominins having large anterior and postcanine teeth (Clarke, 1988; Asfaw et al., 1999) suggests that considerable experimentation in dental proportions characterized Pliocene hominins.

These aspects of dental evolution in *Australopithecus*, *Paranthropus*, and early *Homo* are suggestive of dietary and masticatory diversity, with greater or lesser emphasis on harder, more brittle foods, more abrasive foods, and eventually tougher foods when animal tissues began to contribute to the diet (Teaford and Ungar, 2000; Ungar, 2004).

EXPERIMENTATION IN BODY PROPORTIONS

Essentially nothing is known about limb proportions in the earliest Pliocene hominins. By ~4.1 Ma, *Au. anamensis* showed broadening of the weight-bearing proximal tibia, probably related to habitual bipedal striding (Leakey et al., 1995). *Au. afarensis* (based largely on the AL-288 partial skeleton) exhibited short legs and long arms relative to estimated trunk length, suggesting a locomotor skeleton that combined arboreal climbing and terrestrial bipedality (Johanson et al., 1987). Similarly, the relationship of forelimb-to-hindlimb joint size in *Au. africanus* appears to have been ape-like (McHenry and Berger, 1998). Analysis of limb bones assigned to *Au. garhi* suggests that elongation of the femur preceded shortening of the forearm (Asfaw et al., 1999). If this interpretation is confirmed by further discoveries, it implies that an important shift in limb proportions was initiated in at least one lineage by ~2.5 Ma.

A human-like, elongated femur coupled with an ape-like, long forearm apparently also characterized *H. habilis*. Confusion arises over *H. habilis* in this regard due to earlier analyses of the OH 62 skeleton, which

indicated more ape-like limb proportions than in *Australopithecus* (Johanson et al., 1987; Hartwig-Scherer and Martin, 1991). This finding was a significant factor in the proposal to transfer *H. habilis* to the genus *Australopithecus* (Wood and Collard, 1999). Reanalysis of the fragmentary partial skeletons OH 62 and KNM-ER 3735 (~1.8 to 1.9 Ma) shows, however, that *H. habilis* possessed a modern human pattern of limb shaft proportions, an elongated hindlimb relative to *Au. afarensis* and *Au. africanus*, yet similar brachial proportions to these taxa (Haeusler and McHenry, 2004). Its elongated hindlimb suggests similarities to *H. erectus* and may imply an anatomical commitment to terrestrial bipedality over longer distances.

NEUROCRANIAL EXPANSION

Although there is some evidence for neurocranial (braincase) expansion in hominins from early to late Pliocene, an increase in “relative” brain size is less certain. Data presented by Aiello and Wheeler (1995) and Wood and Collard (1999) indicate a gradual increase in relative brain size, yet one that extended the pattern defined by Old World monkeys and apes. Rapid encephalization was a characteristic of Pleistocene hominin evolution.

GEOGRAPHIC SPREAD WITHIN AFRICA

Key data points in our currently impoverished understanding of Pliocene hominin biogeography include the presence of *Australopithecus* in southern and north-central Africa (*Au. bahrelghazali*) by ~3.5 Ma (Brunet et al., 1995); hominin fossils in the Malawi corridor at ~2.5–1.8 Ma (Bromage et al., 1995); and the appearance of stone tools in North Africa by ~1.8 Ma (Sahnouni et al., 2002). It is unclear if the data points in north-central and northern Africa derive from a prior hominin

presence in these regions (i.e., *Sahelanthropus tchadensis*: Brunet et al., 2002) or reflect the spread of East African populations. As fossils from Malawi (and potentially Mozambique and south-central Africa) may provide evidence of exchanges between eastern and southern Africa, so Uganda and Sudan would appear to be underrepresented in our knowledge of hominin/faunal exchanges with northern and north-central Africa. Despite the inadequate fossil record, at least several episodes of Pliocene faunal and hominin exchanges among distant African regions seem likely (Strait and Wood, 1999), and may indicate significant adaptive responses to environmental events.

DEFINITE STONE TOOLMAKING AND TRANSPORT

The earliest record of stone tools, at ~2.6 Ma, is from East Gona and Ounda Gona South, Ethiopia (Semaw et al., 1997, 2003). Even in these oldest known instances, artifacts are quite richly concentrated. Thus, although commonly thought to indicate the oldest stone tools, these sites actually provide evidence of the oldest stone-tool “accumulations.” It is quite possible that flaked stone was first used and deposited very sparsely across ancient landscapes (without stone accumulation), possibly at lowland cobble sources where primary context is difficult to demonstrate, or at higher-elevation outcrops where burial did not take place. The point is that archeological visibility plays a large role in determining when regular chipping and use of stone tools began (Panger et al., 2002). The date of 2.6 Ma approximates the oldest clustering of stone artifacts brought from diverse lithic sources. This marks a key behavioral transition, the transport of materials over substantial distances to favored locations.

Making stone tools was itself a major adaptive breakthrough, as sharp flakes and pounding implements greatly extended the dental equipment available to hominins. It is

still unclear, though, which (and how many) hominin species were responsible for the Pliocene artifacts, and whether these hominins depended on stone tools episodically, seasonally, or year-round. Late Pliocene toolmaking entailed the use of tools (e.g., hammerstones) to make tools, which may imply a cognitive difference with respect to the use of natural objects or hands-only toolmaking evident in chimpanzees. Further behavioral complexity is seen even in the oldest tool assemblages by the extensive reduction of stone cores and the preferential selection of certain rock types for flaking (Roche et al., 1999; Semaw et al., 2003; Delagnes and Roche, 2005).

Pliocene concentrations of stone tools and animal bones signal one of the oddest developments in human evolution – consumption of food away from its source with significant delay in eating food after acquiring it (Isaac, 1978). The ability to transport things opened up essentially all movable food resources to stone-tool processing. This meant an increase in the complexity of spatial and temporal mapping of resources, and it ultimately had enormous evolutionary consequences for hominins who adopted tool/food transport as a basic way of life. The movement of resources would have allowed Oldowan toolmakers to use tools on widely dispersed foods, to make use of foods that varied considerably in their seasonal availability, and to adjust to changing habitats and resource conditions (Potts, 1991, 1996).

ACCESS TO LARGE MAMMAL CARCASSES

The oldest evidence of hominin interaction with large animal carcasses (size class 3: roughly 100–350 kg) coincides with the first known record of stone tools. Reported instances include a cut-marked equid calcaneum on the surface of site OGS-6 at Gona, Ethiopia, dated ~2.6 Ma (Semaw et al., 2003; Domínguez-Rodrigo et al., 2005); and

cut- and percussion-marked surface bones at Bouri, Ethiopia, dated ~2.5 Ma (de Heinzelin et al., 1999). Although no tools were found with the modified bones at Bouri, sharp stone flakes and cores were directly associated with broken animal bones at Gona. This appears to establish the timing of an important dietary shift toward a high-quality food resource (high energy/protein, low digestive costs), which was patchily distributed and, in general, less predictable in time and space than plant foods. It is unknown, however, whether access to and consumption of large animal tissues (muscle, fat, and nutritious internal organs) during the late Pliocene occurred regularly throughout the year, seasonally, or rarely over a lifetime or many generations. An intriguing insight on this matter may come from the genomal analysis of tapeworms. Human-specific tapeworms had emerged (i.e., distinct from tapeworm lineages specific to African carnivores) between 1.7 and 0.7 Ma; this appears to imply that access to raw or poorly cooked meat by modern human ancestors became sufficiently regular (such that uniquely human tapeworm lineages could evolve) only after 1.7 Ma (Hoberg et al., 2001).

Even the occasional consumption of large herbivore tissues meant that certain Pliocene hominins actively entered the competitive realm of large carnivores, in which predation risks were heightened. Although much attention is paid to tissues from animals >100 kg, an archeological site at Kanjera South (~2.1 Ma) shows that under certain circumstances Pliocene toolmakers focused on smaller animals (Plummer et al., 2001; Plummer, 2004), perhaps indicative of diverse strategies of carcass acquisition dependent on environmental conditions. The sample of late Pliocene sites >2 Ma is not yet large enough to know whether the oldest instances of animal processing typically led to large quantities of meat and marrow or merely to scraps left on abandoned and largely defleshed carcasses. Early access to meat-rich bones and joints

likely had important consequences for hominin social aggregation at least over short spurts of time.

In brief, the acquisition of potentially large packages of meat and fat was one of the seminal events in the record of Pliocene hominin evolution. We do not know how dietarily or socially dependent the toolmakers were on obtaining animal tissues. Whatever the answer, certain Pliocene populations at least occasionally took on the temporal, energetic, and survival costs inherent in the carnivorous domain. This activity minimally involved carrying appropriate stones, maintaining the skill to flake sharp edges, and having the wherewithal to capture and defend animal carcasses for long enough to gain significant nutrition from them. All of the factors noted here – e.g., the means of accessing carcasses, the dietary and social payoffs, the competitive and predation costs – were almost certainly highly sensitive to local environmental conditions and the faunal context (Potts, 2003).

SYNOPSIS OF ADAPTIVE CHANGE IN PLIOCENE HOMININS

As the preceding summary implies, key adaptive shifts in Pliocene hominin evolution occurred mainly in three interrelated domains: *mobility* (indicated, for example, by a change in limb proportions, biogeographic spread between regions, and object transport by toolmakers), *foraging* (indicated by the use and accumulation of flaked stone and hammers in acquiring food), and *diet* (indicated by change in dental proportions and the use of stone tools to access food from large animals). Organisms, in general, respond to environmental variation largely via locomotor, foraging, and dietary adaptations, especially by tracking favored resources or climatic conditions, by altering the amount of time and the strategy of finding food, and by switching to alternative foods when

necessary. Environmental conditions almost certainly would have affected the expression of novel behaviors in these three domains. Thus, studies that aim to relate the Pliocene faunal record to hominin adaptive change may benefit by focusing also on evidence of changing patterns of mobility, foraging, and diet in other large mammals.

Pliocene Environmental Dynamics

Emphasis here will be given to the nonfaunal evidence of Pliocene environments. The main data sources include deep-sea $\delta^{18}\text{O}$ records of benthic foraminifera, African dust records, Mediterranean sapropels, and stable isotope and pollen evidence obtained from hominin localities. The methods by which these data sources contribute to understanding environmental dynamics are summarized in Vrba et al. (1995), Potts (1998b), and deMenocal (2004).

GLOBAL CLIMATE DYNAMICS

The two most significant global climate events of the Pliocene were the onset of significant Northern Hemisphere glaciation (NHG) and a shift in the dominant period of climate oscillation, both of which occurred ~2.80 to 2.75 Ma. Significant NHG was preceded by higher temperature worldwide, an era known as the early Pliocene warm period (EPW), roughly 5.3 to 3.3 Ma (Tiedemann et al., 1994; Shackleton, 1995; Ravelo et al., 2004). During the EPW, global surface temperature was ~3°C warmer than at present, sea level ~10–20 m higher, and atmospheric CO_2 concentrations ~30% greater (Ravelo et al., 2004). ^{18}O enrichment in marine benthic foraminifera beginning in the mid-Pliocene indicates decreased temperature, preferential evaporation of the lighter isotope ^{16}O , and its retention in spreading continental ice sheets. The general $\delta^{18}\text{O}$ trend, therefore, suggests a colder, drier, more glaciated planet since about 3 Ma.

The overall trend, however, was disrupted by periodic reversals – i.e., warming, deglaciation, release of ^{16}O into the oceans, and sea-level rise. In fact, relative to the Oligocene and Miocene, the Pliocene was a time of considerably heightened $\delta^{18}\text{O}$ oscillation – and thus a novel degree of climate variability (Potts, 1998b). The onset of NHG was associated with a change in the period of climate oscillation from predominantly 19–23 Kyr to 41 Kyr, reflecting a shift from orbital precession to obliquity as the overarching determinant of variability in solar heating (insolation).

Tropical and subtropical climate is, of course, particularly relevant to Pliocene evolution in East Africa. According to an analysis of marine records by Ravelo et al. (2004), EPW tropical climate was (unlike today) characterized by weak east–west zonal (Walker) sea circulation, which meant essentially permanent El-Niño-like conditions. Development of strong Walker circulation took place in two steps, neither one temporally linked with the onset of NHG. The first tropical climate reorganization, between 4.5 and 4.0 Ma, was marked by altered surface water gradients and ocean circulation, possibly linked to restriction of the Panamanian and Indonesian seaways. The second, between 2.0 and 1.5 Ma, established strong Walker circulation, a steeper sea surface temperature gradient across the Pacific, and overall initiation of the modern tropical climate system. Thus, while the onset of significant NHG occurred as subtropical conditions began to cool, revisions in the Pliocene tropical climate system were independent to some degree (Ravelo et al., 2004).

Understanding the processes of climate change, especially ocean–atmosphere–land linkages, has become important in exploring the environmental events potentially related to human and faunal evolution in Africa. In particular, geo- and biochemical datasets and climate models have shown that African aridification, in general, is controlled by tropical sea surface temperature (SST), that East

African aridification beginning around 3 Ma was likely controlled by Indian Ocean SST, and that precessional variations in C_3 and C_4 plants have been controlled by changes in monsoonal precipitation driven by low-latitude insolation changes (Goddard and Graham, 1999; Philander and Fedorov, 2003; Schefuß et al., 2003). These findings imply that East African climate change has largely been governed by ocean–atmosphere linkages in the low latitudes, in close proximity to the continental basins where Pliocene hominins are known to have lived.

NORTHEAST AFRICAN CLIMATE DYNAMICS

Despite the strong influence of tropical oceans on East African climate change, shifts in the tempo of climate variability appear to have been tightly linked across tropical-, mid-, and high-latitudes. In particular, East and West African dust records obtained from deep-sea cores (10–14°N latitude) show the shift from precessional (23 Kyr) to obliquity (41 Kyr) dominance at ~2.8 Ma, nearly concurrent with the shift in the $\delta^{18}\text{O}$ record (Tiedemann et al., 1994; deMenocal, 1995; deMenocal and Bloemendal, 1995).

Continental dust records in both regions illustrate three important aspects of Pliocene African climate change: (1) an overall increase in aridity, (2) a change in the periodicity of arid–moist cycles, both at ~2.8 Ma, and (3) the division of overall climate variability into alternating high- and low-variability packets, typically 10^3 to 10^5 years in duration (deMenocal, 2004). While $\delta^{18}\text{O}$ shows a significant and largely permanent rise in the amplitude of temperature and glacial–interglacial oscillation, low-latitude dust records do not clearly show this larger amplitude. What the dust records do show (which is not clearly evident in $\delta^{18}\text{O}$) is a time series of alternating intervals of high and low amplitudes. That is, inter-

vals of high aridity–moisture variability were punctuated by intervening periods of low variability, which deMenocal (2004) postulates resulted from the modulation of precession by orbital eccentricity.

Further evidence of African climate dynamics comes from the eastern Mediterranean record of sapropels, which has vastly improved since 1995 (Comas et al., 1996; Emeis et al., 1996). Sapropels are dark layers enriched in total organic carbon and certain elements such as Fe, S, Si, Ti, and Ba relative to Al (Wehausen and Brumsack, 1999). Sapropels are tied to the intensity of the African monsoon and to precessional periods of highest precipitation and discharge of the Nile into the eastern Mediterranean. The sapropel record indicates that there were peaks in African moisture every ~20 Kyr throughout the Pliocene (Emeis et al., 2000). Sapropels are not preserved in all expected intervals due to oxidation and postdepositional burn-down of organics. However, sapropel “ghosts” are now recognized, and very regular variations in Ba/Al and Ti/Al ratios indicate peaks in biological productivity associated with strongest Nile discharge (Wehausen and Brumsack, 1999, 2000). Geochemical analysis confirms, therefore, that sapropels are only the most visible indicators of a highly robust and rhythmic cyclicality in African climate that persisted through the entire Pliocene and Pleistocene. Sediments that intervene between sapropels (and other layers of high bio-productivity) show heightened levels of continental dust derived during arid intervals from the circum-Mediterranean area, including the Sahara.

Age estimates for each sapropel, sapropel “ghost”, and “red interval” (in which no sapropels are preserved) for four Mediterranean cores, including ODP Site 969 dating between 5.33 Ma and 8 Ka, are given by Emeis et al. (2000), and are based on a standard 3000-year lag between mathematically predicted precession minima and sapropel midpoints (Lourens et al., 1996). Analysis of organic-carbon

concentrations indicate that mid-Pliocene sapropels lasted for about 1,000 to 6,000 years, yet periods of enhanced bio-productivity (defined by Ba enrichment) lasted for 8,000 to 12,000 years (Wehausen and Brumsack, 1999). The latter range currently provides the best estimate for the duration of high African precipitation and Nile discharge during Pliocene precessional cycles. Precessional forcing of low-latitude monsoons was the leading mechanism of sapropel formation even after significant NHG began at ~2.8 Ma; however, the Mediterranean oxygen stable isotope record shows that this mechanism was more strongly affected by obliquity after 2.8 Ma and by 100-Kyr eccentricity cyclicity after 0.9 Ma (Emeis et al., 2000). The modulation of precession by obliquity and eccentricity yields a monsoon index, which has proven useful in predicting periods of highest African precipitation and sapropel formation (Rossignol-Strick, 1983).

For investigators of East African faunal and hominin evolution, the obvious question is whether the regular tempo of high precipitation and intervening aridity (as captured by the eastern Mediterranean sapropel record) and of northern African aridity–moisture cycles (as indicated by the deep-sea dust record) actually reflects the tempo and nature of climate change south of the Horn of Africa and the Sahara. That is, are the dust and sapropel findings strongly representative of Pliocene climate change associated with fossil sites in Kenya and Tanzania, for example?

This question is ultimately best answered by careful study of the timing and extent of high-moisture and high-aridity intervals in East Africa (e.g., Ashley and Hay, 2002; deMenocal, 2004). Tephrocorrelations between the Turkana basin and Gulf of Aden do suggest, though, a direct means of linking the dust record to broader East African climate change (deMenocal and Brown, 1999). Furthermore, Nile discharge is controlled by the African monsoon, in which moisture originating in the South Atlantic Ocean is captured by the Nile drain-

age. The intensity of the monsoon is known to be influenced by the meteorological equator, known as the intertropical convergence zone (ITCZ), and by trade-wind intensity – both of which influence a much broader portion of Africa than the Nile catchment (Emeis et al., 2000). For these reasons, both the sapropel and dust records appear to offer a good approximation of the tempo and degree of climate variability over East Africa, and offer specific predictions about the age of alternating arid and humid intervals throughout the region.

An intriguing hypothesis proposed recently is that precessional variation in moisture responsible for sapropel formation has also controlled depositional–erosional cycles in continental basins of northeastern Africa (Brown, 2004). Thus, the deposition of fossiliferous Member 1 in the Omo Kibish Formation, following a substantial erosional period, has been considered contemporaneous with the wet interval of sapropel S7; on this basis and Ar/Ar dating constraints, the date of this sapropel at ~195 Ka has been assigned to the early *Homo sapiens* fossils from Kibish (McDougall et al., 2005). If this hypothesis proves to be correct, it means that major depositional–erosional sequences in East Africa may be linked to climate variability. One unresolved issue is that major erosional periods, in which massive amounts of sediment must be moved, would also seem to require substantial water flow, which could be linked to significant monsoonal precipitation rather than to arid times. Nonetheless, since fossils are preserved during depositional intervals, the hypothesis linking depositional–erosional intervals with climate variability could have important implications for analyses of the fossil record.

ENVIRONMENTS ASSOCIATED WITH PLIOCENE HOMININ LOCALITIES

Fieldwork at Pliocene sites has rarely focused on environmental dynamics; the standard goal, rather, has been to reconstruct the habitats

reflected in particular strata in which fossils or archeological remains are found. For example, based on stable carbon isotopic records, fauna, and fossil seeds, WoldeGabriel et al. (1994, 2001) concluded that late Miocene and early Pliocene hominins of the Middle Awash, Ethiopia, lived in woodland and forest, and that early hominins inhabited more open vegetation only after 4.4 Ma. By contrast, a mosaic of open and wooded habitat is reconstructed by Leakey et al. (1996) for the upper Nawata Formation at Lothagam, Kenya, near the Miocene–Pliocene boundary, though hominin fossils are rare at Lothagam. Similarly, regarding the mid-Pliocene, Leakey et al. (2001) interpret the environments associated with *Australopithecus* and *Kenyanthropus* in Kenya, Tanzania, Ethiopia, and Chad as a patchwork of habitats that included open grassland, woodland, and gallery forest.

Cerling (1992; Cerling et al., 1988) and more recently Kingston (Kingston et al., 1994), Quade (Quade et al., 2004), and Wynn (2004) have developed a different approach, which is to establish a chronological record of carbon and oxygen stable isotope values for paleosol carbonates. This type of research has provided temporal sequences of vegetation structure related to carbonate precipitation in at least seasonally dry soils. The paleosol carbon stable isotope ($\delta^{13}\text{C}$) record, then, primarily detects habitats that are sufficiently arid for carbonate to precipitate and be preserved.

Wynn (2004) synthesizes $\delta^{13}\text{C}$ values beginning ~4.3 Ma for northern Kenya (Kanapoi, East and West Turkana). Although paleosols are abundant in certain time intervals, the combined stratigraphic record preserves evidence of lengthy unconformities and several lacustrine intervals, which may indicate relatively wet times. The Turkana $\delta^{13}\text{C}$ record shows, nonetheless, an overall increase in C_4 vegetation and aridity particularly at ~3.58–3.35, 2.52–2, and 1.81–1.58 Ma. These times of increased $\delta^{13}\text{C}$ values are associated with higher variance in $\delta^{13}\text{C}$, suggesting that an increase in vegetation spatial variability

occurred over time as climatic instability also increased.

Although paleosol carbonate $\delta^{13}\text{C}$ provides a superb environmental record, the intermittent formation of paleosols over time (i.e., periods of relative landscape stability) and the fact that carbonate precipitation depends on certain climate conditions make it impossible to obtain a time series of samples that is systematic (e.g., evenly spaced) with regard to time or stratigraphic thickness. As a result, it is difficult to place the long-term East African record of increasing aridity – essentially the story of paleosol $\delta^{13}\text{C}$ – in the context of climate oscillation – also a vital dimension of the Pliocene environmental picture. The obvious solution is to seek the ways in which oscillatory records (e.g., African dust) and progressive aridity records (such as paleosol $\delta^{13}\text{C}$) add both complementary and different kinds of information to our knowledge about Pliocene environmental change. While the terrestrial deposits in African basins offer less-complete and less-continuous environmental records, they also provide substantial evidence of regional and local tectonic activity, including volcanism, which added significantly to the environmental dynamics faced by East African hominin populations and fauna (Feibel, 1997).

Analysis of a high-resolution sequence of fossil pollen at Hadar by Bonnefille et al. (2004) provides one of the only studies of East African climate dynamics at a Pliocene hominin site. Based on detailed analysis of modern and fossil pollen samples, this study derived estimates of temperature, precipitation, humidity, and vegetation structure (biomes) associated with *Au. afarensis* at Hadar, ~3.4–3.0 Ma. The sequence of regional habitat through the Hadar Formation was reconstructed as follows, starting ~3.4 Ma and ending ~2.95 Ma: forest, wet/dry grassland, forest, woodland, wet grassland, dry grassland, and woodland. The deposits yielded, as expected, a discontinuous and uneven sequence of fossil pollen with the exception of a single ~20-Kyr interval. This densely sampled interval (approximately

1 pollen sample per 1 Kyr) recorded significant cooling ($\sim 5^{\circ}\text{C}$), a precipitation increase (200- to 300-mm per year), and much greater forest cover at ~ 3.3 Ma – i.e., contemporaneous with a global marine increase in $\delta^{18}\text{O}$ (indicative of cooling). This is the first case where habitat variability has been measured with sufficient resolution in Pliocene deposits of eastern Africa to demonstrate its correspondence with global climate variability. Bonnefille et al. (2004) note that *Au. afarensis* fossils occur in stratigraphic intervals that also record, according to the fossil pollen, substantial fluctuation in the relative extent of forest, tropical and temperate woodland, and grass cover.

While fossil mammals are often useful in deriving habitat reconstructions (e.g., Reed, 1997), they also provide insights about environmental dynamics. For example, Bobe et al. (2002) and Bobe and Behrensmeyer (2004) document a shift in late Pliocene faunal variability (the relative proportions of bovids, suids, and primates) in the Turkana basin. The shift is from relative stability (~ 2.8 to 2.6 Ma) to higher variability with a periodicity of about 100 Kyr, beginning ~ 2.5 Ma. It is not yet clear what the 100-Kyr periodicity reflects; at face value, it could indicate that faunal dynamics were more sensitive to the weak eccentricity modulation of precession than to the more rapid, precessional- and obliquity-scale variability that dominated tropical and subtropical Africa during the Pliocene. One of the interesting points of this study is that the transition to high faunal variability is associated with the first appearance of *Homo* (based on dental evidence from Omo) and stone tools in the Turkana basin (Bobe et al., 2002).

Hypotheses Relating Environmental Dynamics, Hominin Evolution, and Faunal Change

All hypotheses that seek to relate environment and evolutionary change ultimately depend on an understanding of climate and tectonic

dynamics. We have seen that Pliocene climate change involved a distinct trend – namely, cooler, more arid conditions, and significant NHG, beginning ~ 2.8 – 2.75 Ma. The Pliocene can also be divided into a period of long-term environmental stability – the EWP between 5.3 and 3.3 Ma – and a period of higher amplitude climate oscillation associated with the shift from precessional- to obliquity-dominated insolation variability after ~ 2.8 Ma. There is also initial evidence of alternating shorter-term packets of high- and low-climate variability throughout the Pliocene, at least in Africa.

In general, then, there are three ways in which environmental dynamics and evolutionary change may relate to one another. In Figure 1, an episode of evolutionary change (shaded vertical bars) refers to the first or last appearance of a particular adaptive character or complex, the first or last appearance of a lineage, or a well-defined increase in the rate of change in a morphological character or suite of traits. One possibility (Hypothesis A) is that such episodes of evolutionary change are unassociated with any environmental change. In this case, evolutionary events may result from internal population dynamics, ongoing resource competition, predation, disease, or other factors that operate in many different settings, and possibly at all times. Thus, evolution may occur even during times of relatively stable environment (low-climate variability). Another possibility (Hypothesis B) is that evolutionary change is correlated with, and causally related to, a progressive shift in environment. The primary evolutionary mechanisms at play in this hypothesis are directional selection and population vicariance. The former leads to the origin of novel adaptations and behaviors, the latter to a greater probability of speciation or extinction. A final possibility (Hypothesis C) is that evolutionary change is stimulated by rising environmental variability, or takes place over several periods of high-climate/resource variability interspersed with periods of low variability. The primary mechanism postulated

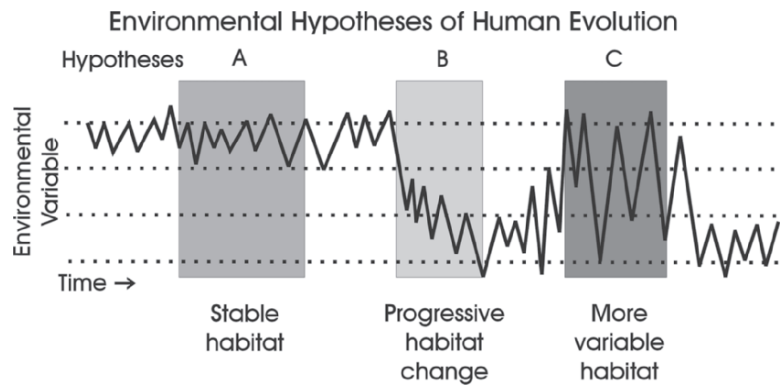


Figure 1. Three hypotheses relating evolutionary and environmental change: **Hypothesis A:** Evolutionary change (first vertical bar) is unconnected to environmental change. It takes place at any time, including intervals of environmental stability or low variability. Newly evolved traits may reflect, for instance, ongoing competition within or between species irrespective of environmental setting. **Hypothesis B:** Evolutionary change (second vertical bar) is concentrated in relatively brief periods of directional environmental change (e.g., a stepped decrease in temperature or precipitation). Newly evolved traits or taxonomic turnover directly reflects the shift from one dominant habitat type to another. **Hypothesis C:** Evolutionary change (third vertical bar) is concentrated in intervals of high environmental variability. New traits reflect greater adaptive versatility, and first/last appearances of taxa reflect increasing vicariance or resource variability during these intervals. These hypotheses are ideally testable if the record of hominin fossils and behavioral artifacts were relatively continuous and if the samples were densest around the time of a shift in the direction or variability of environmental change.

to explain this type of evolution-environment correlation is variability selection – i.e., a hypothetical process of genetic selection that results from increasing habitat/resource variability over time and results in improved environmental adaptability.

As Figure 1 implies, temporal association (coincidence in time) is the key to all tests of how instances of evolution and environmental change causally relate to one another. As much as we realize that “correlation does not equal cause,” we are stuck with tests of coincidence in trying to determine the causes of events in virtually all historical sciences. Temporal association alone is insufficient, however; it is also important to specify compelling evolutionary factors and processes by which different types and tempos of environmental change may have stimulated certain types of adaptive change and speciation/extinction events. In other words, the theoretical underpinnings of an evolutionary explanation and the data pertaining to the coincidence of events (climatic and evolutionary) are both critical to consider.

For this reason, many (but not all) of the environmental hypotheses previously proposed to explain evolutionary change in Pliocene hominins and faunas have also hypothesized particular mechanisms linking the two.

Table 1 offers a synopsis of seven hypotheses (and test expectations) that have given focus to research on Pliocene evolutionary change in recent years. These ideas are divided into two types: adaptation hypotheses (which relate to the origin of adaptations) and turnover hypotheses (which relate to major turnover events – species originations and extinctions).

A variant of the turnover-pulse hypothesis, referred to as the “relay model” (Vrba, 1995a), partly derived from Vrba’s (1992) “habitat theory”, considers adaptation an integral part of explaining turnover. But there is an interesting difference from Vrba’s original turnover-pulse hypothesis (Vrba, 1988). In the relay model, the interval of concentrated FADs and LADs may actually be quite broad, spanning several hundred thousand years, rather than essentially instantaneous. The reason is

Table 1. Summary of hypotheses relating environmental and evolutionary change (adaptive evolution and species turnover)

Environmental hypotheses related to adaptive evolution

1. **Habitat specific:** A specific type of habitat was necessary for a particular adaptation or suite of adaptations to emerge in one or more lineages. Examples: savanna hypothesis (e.g., Klein, 1999: 248–252), riparian woodland scavenging model (Blumenschine, 1987).

Test expectations: FAD for the adaptation (i.e., a functional morphological, dietary, or archeological proxy) is correlated in time and space with a specific paleohabitat. This association between the adaptation and the specific habitat is consistent in time and space and is maintained for a significant period of time. The functional or behavioral consequences of that adaptation make sense as a response to that specific habitat type.

2. **Directional change:** A particular adaptation evolved in one or more lineages as the direct result of a major progressive change in habitat – e.g., from moist forest to dry, open conditions (e.g., Vrba et al., 1989), or from warm to cool conditions (e.g., Vrba, 1994).

Test expectations: FAD for the adaptation is temporally constrained to a well-defined period (e.g., <100 Kyr) of significant directional environmental change, evident in one or more proxies of temperature, vegetation, etc. If the directional change reflects an ongoing environmental trend (e.g., lasting >500 Kyr), the FAD for the adaptation occurs near the initiation of that trend. The functional or behavioral shift in adaptation makes sense as a response to the newly emerging habitat.

3. **Variability selection:** A particular adaptation evolved in one or more lineages as the direct result of a significant increase in environmental variability (in time and/or space), which resulted in large variability in the adaptive conditions pertinent to those lineages (Potts, 1996, 1998a, b). Examples: earliest hominin bipedality and earliest tool/food transport emerged as adaptations to wider variability in vegetation (locomotor substrates) and in food availability (Potts, 1996); making stone tools and the adaptations of earliest *Homo* were related to heightened variability in mammalian faunas (Bobe and Behrensmeier, 2004).

Test expectations: FAD for the adaptation is temporally correlated with well-defined intervals of high variability in the landscapes, food resources, or overall adaptive settings where that adaptation is first evident. The adaptive change makes sense as a response to environmental instability/uncertainty – i.e., it assists a lineage in persisting across large environmental shifts (e.g., major and repeated change in moisture and/or temperature; episodic large tephra events over broad landscapes).

3A. **Adaptability:** A particular adaptation or suite of adaptations enables a lineage to persist across larger environmental shifts than those survived by prior lineages.

Test expectations: A novel adaptation or suite of adaptations occurs in (or spreads to) a wider diversity of environments than prior adaptations (characteristic of earlier lineages) are known to occur. The LAD of an adaptation (or the lineage bearing it) corresponds with a significant increase in environmental variability. This represents evidence that large environmental change is a significant factor in the survival of an adaptation and the evolution of novel functions that replace or add to it.

Environmental hypotheses related to species turnover

4. **Turnover pulse:** The origination and extinction of numerous species occurs as a result of major climate change (climate forcing of evolution), which increases overall habitat and population vicariance – and thus stimulates turnover (Vrba, 1980, 1988).

Test expectations: Lineage FADs and LADs should be concentrated in a tightly constrained interval of climate change. The adaptations of new and terminal species during the interval of climate change should reflect the overall environmental trend (e.g., during climatic drying, there is a biased origination of arid-adapted taxa and biased extinction of moist-adapted taxa).

4A. **Relay model of turnover pulse:** Within an interval of major climate change, turnover occurs sequentially based on existing adaptations (the breadth of resource use) that prevail within clades (Vrba, 1992). That is, lineages of organisms respond to environmental change with lag effects. Thus, organisms disadvantaged by a major climate trend (e.g., cool-adapted species in a warming trend) tend to become extinct first, followed by speciation in disadvantaged lineages, followed by both extinction and speciation in organisms favored by that trend (warm-adapted species in a warming trend) (Vrba, 1995a).

Test expectations: As in the turnover-pulse hypothesis but with FADs and LADs distributed over a broader period, according to how the diverse adaptations of organisms relate to the overall direction of major climate change.

5. **Prolonged turnover:** Lineage turnover is not pulsed but spread out over time due to the mosaic distribution of vegetation (e.g., patches of woodland persist during the spread of arid grasslands) and the diverse adaptations of organisms. Example: even during major global climate change, the Turkana basin exhibited a prolonged turnover of species between 3 and 2 Ma, with dry- and moist-adapted mammalian species persisting throughout the interval (Behrensmeier et al., 1997).

Test expectations: Even in periods of climate change, species FADs and LADs are distributed over a prolonged time, with small spikes but no single pulse. Turnover and large change in species diversity may be concentrated substantially after the onset of the climate trend if species diversity and ecological diversity are maintained within a region. Even lacking evidence of a turnover pulse, however, significant shifts in species abundance can be tightly correlated with the onset of climate change (Bobe et al., 2002).

that species that exploited different diets and resource diversity are likely to respond to environmental change at different rates, with an offset between the timing of extinction and origination events depending on those adaptations. The idea of a “pulse” that is potentially spread out over several hundred thousand years, as implied by the relay model, poses significant challenges in demonstrating a precise correlation between faunal and climate change.

The main competing explanation is what I have termed the prolonged-turnover hypothesis, the best recent example of which is given in the Turkana basin study by Behrensmeyer et al. (1997). A critical link between pulsed- and prolonged-turnover hypotheses is provided by Bobe’s analysis of taxonomic abundance patterns in the Turkana basin. His study shows that the relative *abundance* of taxonomic groups may be quite sensitive to the onset of major climate change, even if species-level turnover is less so (Bobe and Eck, 2001; Bobe et al., 2002).

The variability selection (VS) hypothesis also has ramifications in the realm of faunal turnover (Bobe and Behrensmeyer, 2004), yet it was originally developed as an explanation of adaptive change (Potts, 1996, 1998a, b). The concept of VS is that environmental variability plays a substantial role in the process of evolving adaptive functions, novel behaviors, and plasticity in all biological systems (Potts, 2002). This process of originating adaptive features is a response to environmental dynamics, the degree and rate of variability in adaptive conditions as played out in a temporally continuous spectrum of environmental change – from milliseconds (in the cellular and physiological realm) to daily to seasonal to decadal, millennial, and orbital time frames.

The radical implication is that a novel trait or biological function may arise as an adaptation to resource uncertainty and unpredictability in the conditions of survival and reproduction rather than as a solution to a specific, constant environmental stimulus or adaptive challenge. The distinction, then, is

whether adaptations evolve mainly in response to specific manifestations of the environment (and overall changes in state from one manifestation to another) – or in response to environmental *dynamics* in all its messy, nested complexity. In the former case, the functioning of an organism reflects the sum or average of past habitats and resource templates. But in the latter case, the functioning of an organism reflects past environmental dynamics, which have shaped the organism’s capacity to adjust to changing resource configurations, disturbances, and even novel settings – all of which define the *adaptability* of that organism.

Thus in Table 1, I define an offshoot of the VS idea, called the adaptability hypothesis. It is the flip side of the VS coin, reflecting the idea that organisms are adapted to a certain range and pace of environmental variability, expressed over the wide spectrum of time scales. The resulting dimensions of adaptability (genomal, developmental, physiological, behavioral, ecological) enable certain adaptations (and lineages) to persist across a surprising variety of environmental transitions and to disperse across a range of habitats, including settings that are unprecedented in an organism’s past.

VS implies, however, that adaptive versatility can be “ratcheted up” in the face of even greater environmental variability. In this event, certain suites of adaptations can be lost, replaced by novel suites that improve the adaptable properties of later organisms. Thus, one of the test expectations of the adaptability hypothesis concerns *last* appearances. That is, the last appearance of a particular anatomical complex or behavior (e.g., combined terrestrial bipedal and arboreal activity in *Au. afarensis*) should coincide with a significant rise in environmental variability. (In this example, extinction of *Au. afarensis* may indeed take place after 2.9 Ma, associated with a rise in African climate variability [deMenocal, 2004].) This loss is then followed by the first appearance or spread of innovations that enhanced adaptive versatility. (Dietary breadth in the masticatory

powerhouse *Paranthropus* and the origin of, or greater reliance on, stone tools in one or more hominin lineages may both qualify as hypothetical examples.)

The fact that certain taxa (e.g., *Au. afarensis*) and adaptive characteristics (e.g., megadontia in *Paranthropus*) endured over several hundred thousand years implies that Pliocene lineages and adaptations were typically static (or, rather, morphologically variable within certain limits) in relation to climate dynamics. The same is true for other mammalian lineages and associated sets of taxa. This observation leads to two questions that continue to challenge paleontologists: First, under what environmental conditions did *substantial reorganization* of adaptive complexes, characters, and faunal associations take place during the Pliocene? Second, why did certain adaptive traits, lineages, and faunal associations persist over periods greatly exceeding the dominant periodicities of Pliocene environmental change?

Future answers to these questions will help us better understand the processes of adaptive, phylogenetic, and ecological change – and particularly the role of environmental dynamics in deciding the balance between persistence (adaptability) and evolutionary innovation.

Faunal Community Evolution

A final hypothesis relevant to Pliocene human and faunal evolution comes from the study of species assembly. Species assembly concerns the co-occurrence of species populations in a given locale. The study of species assembly focuses on the processes that govern which particular taxa are found together and their relative abundances – two aspects of what is typically meant by a faunal community (Belyea and Lancaster, 1999; Hubbell, 2001). While increasingly considered in the biogeographical and ecological literature, the concept of species assembly has barely entered the realm of mammalian paleoecology.

For modern communities, the factors that govern the assembly of species in a local setting fall into three classes. The first – *environmental constraints* – concerns the fact that animals living together (and those species excluded from a given locality) are determined by climate, substrate, vegetation, and other characteristics of the local setting. The second – *internal dynamics* – highlights the role of competition, i.e., certain taxa may be recorded in a given place, and others excluded, based on the competitive ability of species populations in a given setting. The third class of factors – *dispersal constraints* – emphasizes that mobility and random geographic factors, such as habitat corridors and incumbency (those species already present in a particular place), may determine which particular species happen to become part of a local community.

To illustrate the analysis of species assembly and its potential relevance to Pliocene and Pleistocene faunal research, I will draw on an example of faunal and environmental change in the mid-Pleistocene Olorgesailie Formation, southern Kenya Rift Valley (Potts, 1996; Potts et al., 1999; Potts and Teague, 2003, in preparation). Although this faunal sequence ranges from ~1.2 to 0.5 Ma, the analysis of mammalian taxa at Olorgesailie suggests an interesting hypothesis important to examine also in Pliocene contexts.

Figure 2 shows the relative abundance of major taxonomic groups in three *in situ* mammalian fossil samples from the Olorgesailie Formation. These faunal samples were obtained by excavations and surface surveys of three widely exposed stratigraphic intervals: UM1p (upper Member 1 paleosol), LM7s (lower Member 7 sand), and M10/11 (Member 10 and lower Member 11). The stratigraphic section (Potts et al., 1999; Behrensmeyer et al., 2002) and tephra and magnetostratigraphic ages (Deino and Potts, 1990; Tauxe et al., 1992) show the temporal separation between the samples.

The Olorgesailie faunal samples are peculiar in a number of respects. First, all of them exhibit lower proportions of bovids than expected. In

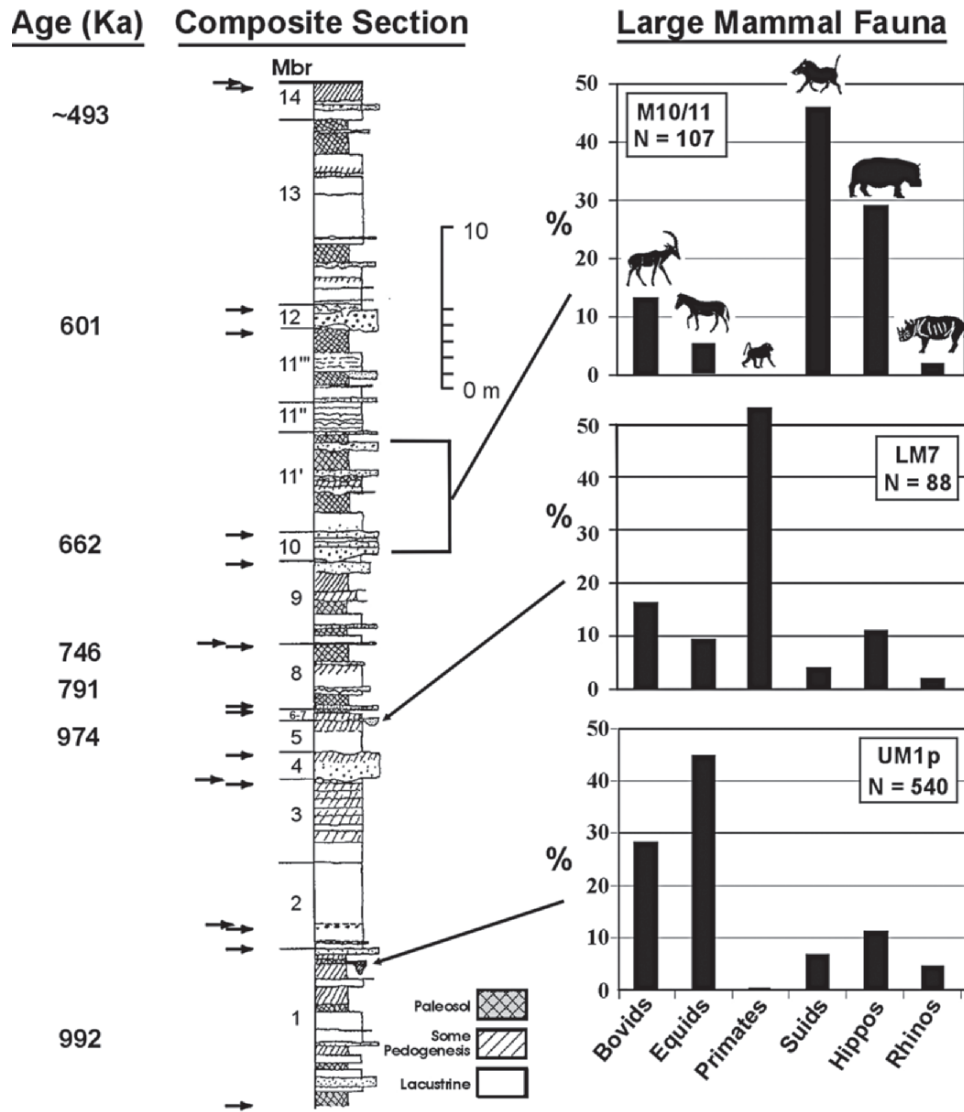


Figure 2. Mid-Pleistocene fauna and environmental change as recorded in the Olorgesailie basin, southern Kenya. Percentage representation (relative abundance) of major groups of large mammals is shown (right) for three fossil samples excavated from relatively narrow time intervals. The three samples are named UM1p, which is a paleosol ~990 Ka in Member 1 of the Olorgesailie Formation; LM7, which is a fluvial sand ~900 Ka in the base of Member 7; and M10/11, which is a series of sand and gravel layers ~662 to 650 Ka in Member 10 and lower Member 11. For the LM7 and M10/11 samples, N is based on minimum number of individuals due to the presence of partial skeletons; for UM1p, N is based on number of individual specimens. The horizontal arrows next to the composite section indicate the stratigraphic positions of major (basin-wide) events of landscape remodeling, which form an important context of mammal community assembly and disassembly. Composite section by A.K. Behrensmeyer and R. Potts (Potts et al., 1999; Behrensmeyer et al., 2002); age estimates based on Deino and Potts (1990) and Tauxe et al. (1992).

none of the three samples do bovids comprise the dominant group of large mammals – in contrast to most other Pleistocene and Pliocene faunal samples in East Africa. A second oddity concerns the relay of taxonomic dominance,

with *Equus* spp. (especially *E. oldowayensis*) as the most abundant large mammal in UM1p giving way to *Theropithecus oswaldi* and *Equus* spp. in LM7s, followed by the dominance of *Hippopotamus* spp. (especially *H. gorgops*) and

the suids *Kolpochoerus* and *Metridiochoerus* in M10/11.

The main questions are: What factors were responsible for this unusual progression? Is Olorgesailie odd relative to other mid-Pleistocene faunal samples in Africa? Was the relay of dominant taxa the result of continuous faunal change within the southern Kenya rift?

To help answer these questions, the first step was to assess how different the mammalian taxa at Olorgesailie were from other mid-Pleistocene faunal samples. Since Olorgesailie taxonomic abundances (Figure 2) are derived from detailed excavations, comparisons with other (typically surface collected) samples required working with species lists only (Potts and Teague, 2003, in preparation). Taxonomic lists from sub-Saharan fossil localities, dated ~1.4 to 0.4Ma, were combined to establish a minimal “geographic species pool” (GSP) pertaining to the mid-Pleistocene of East Africa.

The GSP represents an estimate of the entire population (or metapopulation) from which the local combinations of mammalian species in the Olorgesailie basin were drawn.

In our initial analysis, the mid-Pleistocene GSP consists of 87 species from 17 fossil localities. Various avenues of multivariate analysis, such as detrended correspondence analysis and clustering routines, show that the combinations of taxa found in these 17 localities comprise robust geographic groupings rather than temporal groupings. Figure 3 illustrates one example from many analyses showing the four distinct geographic clusters that consistently result from this study: south-central Africa, the southern Kenya Rift Valley, the Horn of Africa, and Bed IV Olduvai.

In none of the analyses are the individual fossil samples from Olorgesailie any more unusual in terms of their member taxa than other African mid-Pleistocene samples. The

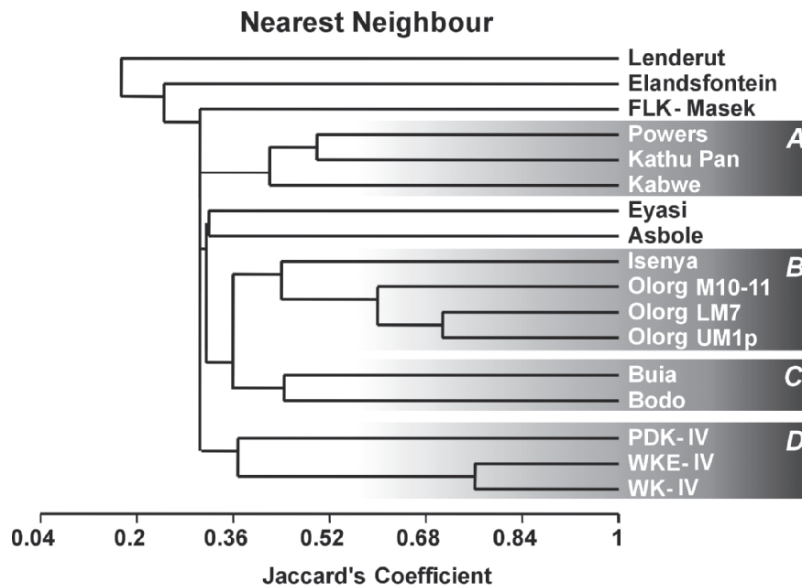


Figure 3. Cluster analysis of mid-Pleistocene mammalian fauna based on taxonomic lists from 17 localities (named on the right). The combined faunal list ($N = 87$ species) represents a minimal estimate of the geographic species pool for sub-Saharan Africa from ~1.4 to 0.4Ma. This analysis used Jaccard's coefficient and nearest neighbor. Other distance measures (e.g., Euclidean) and clustering techniques (paired-group averages) gave similar results and consistently defined four main geographic groupings, indicated here by the shaded areas: A. South-central Africa; B. Southern Kenya Rift Valley, including Olorgesailie; C. Horn of Africa; and D. Olduvai Gorge. None of the cluster analyses produced consistent relationships between the other (nonshaded) samples, and none showed a clustering of fossil assemblages according to their temporal sequence (Potts and Teague, 2003, in preparation).

three Olorgesailie assemblages, in fact, always aggregate in the middle of each cluster analysis or correspondence analysis rather than on the periphery (Figure 3; Potts and Teague, 2003; in preparation). Olorgesailie, therefore, does not appear to be odd with regard to having unique faunal characteristics. Only when a larger number of faunal samples have been collected carefully with adequate taphonomic control, and from as wide a range of depositional contexts as each Olorgesailie sample, that this comparative analysis can be pursued further.

These initial findings suggest nonetheless that geographic factors (dispersal constraints) helped to shape each fossil assemblage in the different basins and regions. Yet this conclusion fails to explain the relay of taxonomic dominance (based on species abundance) in the Olorgesailie basin. Environmental analysis of the Olorgesailie sequence offers an illuminating clue, however: As indicated by the horizontal arrows in Figure 2, the Olorgesailie region was susceptible to repeated basin-wide revamping of the landscape and its resources. The arrows indicate the stratigraphic positions at which dramatic environmental transitions occurred, including large eruptive (tephra-depositing) events, abrupt drying of the lake, replacement of a fluvial-dominated by a lake-dominated landscape, and shifts between periods of sediment aggradation and erosion (or stability, marked by widespread soil formation). These represent the type of environmental events that would have temporarily killed off the herbaceous vegetation (in the case of the tephra events) or substantially altered local climate and the availability of water and other food resources.

I would offer, then, the following hypothesis: Basin-wide environmental events of sufficient magnitude can lead to the breakdown of mammalian communities. That is, during substantial environmental events, species populations must emigrate from the basin or die out locally, and as a result, the taxonomic community at least temporarily

dissolves – i.e., the community disassembles – followed by a subsequent period of species reassembly. Each period of reassembly is an experiment in which the factors typically thought to explain taxonomic combinations (environment, competition, and dispersal) once again intersect and play a role. Yet the instability created by climate dynamics and tectonic events is the critical factor causing recurrent episodes of community assembly and disassembly.

The focus on environmental dynamics in this community assembly–disassembly hypothesis is not meant to undermine the importance of taphonomic biases and time averaging in explaining the variations that may occur among fossil samples. Assessing such biases is a critical first step in the analysis of species co-occurrence and the differences between fossil samples. In the case of Olorgesailie, variations in species body size, skeletal part durability, and depositional environment do not play a significant role in explaining the differences between samples. Variation in time averaging also appears to play a smaller role than ecological factors in explaining the taxonomic differences (Potts and Teague, 2003, in preparation).

The point is that environmental dynamics can disrupt faunal continuity within a basin. This hypothesis challenges, therefore, the assumption that the sequence of mammalian fauna within a basin reflects *in situ* faunal turnover or a local succession of taxa due to adaptive change. Hypotheses like turnover pulse and prolonged turnover often assume the continuity of the fauna within a basin (or region) over time. The possibility of recurrent community assembly and disassembly implies, however, that faunal variation over time and space may reflect environmentally driven experimentation in how random and adaptive factors play out on a larger biogeographic scale.

The Olorgesailie example begs the question, was the Pliocene of Africa the same as

the mid-Pleistocene? Given that global climate oscillation after ~900 Ka involved higher amplitude and longer periodicity, an intriguing possibility is that Pliocene faunas experienced significantly lower magnitudes of disturbance due to climate. The apparent heterogeneity of mid-Pleistocene mammalian communities in time and space may also reflect very limited connectivity among distant basins. It is possible, however, that during the Pliocene, basins in different parts of Africa would have served as viable species reservoirs for repopulating areas affected by large environmental events. This would have been possible as long as there was strong connectivity among the distant basins. An obvious test of this idea is to see whether mammalian communities were reassembled with approximately the same species at similar relative abundances before and after large events, such as the eruption of the Tulu Bor Tuff (Turkana) and Sidi Hakoma Tuff (SHT) complex (Hadar) at ~3.4 Ma.

The final point of the Olororgesailie example concerns the hominin toolmakers. The early humans responsible for making Acheulean hand axes were consistently present; they deposited their lithic debris immediately below and above almost all of the stratigraphic boundaries marking basin-wide environmental impacts. This suggests that while mammalian species, in general, had varying success in reestablishing themselves after major environmental transitions, the hominins were nearly always able to survive locally or at least to rapidly colonize the Olororgesailie basin after a disruption.

The assembly–disassembly hypothesis thus leads to interesting and relatively novel directions in mammalian paleoecology, with considerable relevance to Pliocene studies: It demands better documentation of environmental dynamics in terrestrial sequences; improved estimates of environmental impacts on local communities; new analyses of geographic species pools and fauna provinciality; and the comparison of

how successful hominins and other mammals were in adapting to recurrent ecological disturbances. Eventually, this hypothesis may better our understanding of paleoecological and evolutionary processes at diverse temporal and spatial scales.

Conclusion

The Pliocene was a 3.5-million-year period of appreciable species turnover and adaptive change apparent in hominins and other large mammals. It was also a time of marked environmental change – in particular, a substantial decrease in global temperature, the onset of NHG, heightened African aridity, a significant rise in climate oscillation, and episodic remodeling of African landscapes inhabited by hominins and other organisms. How these data sets regarding environmental and evolutionary change fit together represents a significant and challenging research agenda.

One area of this agenda needs vast improvement – namely, stratigraphic precision in correlating faunal change, evolutionary events, and environmental dynamics. Paleoenvironmental analysis of early human sites in East Africa has paid hardly any attention to environmental dynamics *per se*. Research has instead focused on the environments of particular stratigraphic intervals that also contain hominin fossils. Yet in many instances, the scientists responsible for the paleoenvironmental analysis and those responsible for the early human discoveries locate their evidence in different strata (Copes and Potts, 2005). Typically, then, there is a stratigraphic (and temporal) offset between the two lines of evidence. This offset greatly thwarts our ability to test environmental hypotheses of human evolution, which depends on examining the co-occurrence of past events in time and space.

Even where there is stratigraphic overlap, the environmental and fossil data may represent

time-averaged data sets of >100 Kyr (e.g., Leakey and Harris, 1987; Bobe et al., 2002). This degree of temporal resolution inherent in most East African data sets makes it difficult, at best, to determine how precisely faunal and hominin evolutionary change matched up against specific environmental shifts and the precessional- to obliquity-scale tempo of African Pliocene climate change. A major challenge ahead is to acquire long-term evidence of faunal variation and environments from continental basins that can be compared against the ~20- and 41-Kyr periodicities of Pliocene climate variability.

A second area marked for future attention is the matter of spatial scale. Different aspects of ecological and evolutionary processes are likely to be learned by comparing diverse spatial and temporal scales (Wiens et al., 1986). Intrabasin comparison can document not only faunal heterogeneity through time but also habitat patchiness within a single narrow time interval (e.g., Potts et al., 1999). Analyses confined to a single basin can, however, lead to incorrect generalizations about preferred hominin habitat, overall taxonomic diversity and abundance, and faunal turnover during the Pliocene. Consideration of several basins within a region offers an opportunity to compare environmental, including faunal, sequences, and thus provides a way of dissecting local versus regional causes of faunal change. Interregional comparison – e.g., across eastern, southern, and north-central Africa – allows researchers to assess continent-wide influences on faunal dynamics and to examine the processes of how local communities were derived from the larger geographic species pool. Finally, comparison between continental and marine climate records represents the broadest spatial scale in which to view the environmental causes of faunal change in the Pliocene.

Most previous considerations of hominin evolution have tended to treat “the environment” in a monolithic sense. The aim of

including diverse spatial and temporal scales in our analyses averts this over-simplification of the spatio-temporal complexity of environments in which Pliocene mammals, including hominins, lived and evolved. In the end, all tests of hypotheses about Pliocene environment, faunal change, and hominin evolution are matters of scale.

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