Role of Environmental Stimuli in Hominid Origins

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Contents

Abstract

Environmental stimuli have influenced the evolution of hominins and other mammals at the levels of ontogeny, organismal adaptation, and speciation. The review refers to some agreement which has emerged – as well as to

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persistent debates – on the issue of environmental linkages to hominin adaptation. Current hypotheses which link physical change, adaptation, and speciation in general and in hominins in particular are discussed (including hypotheses on the role of ecological specialization and generalization, the coordinated stasis and variability selection hypotheses, habitat theory, and the turnover pulse hypothesis). Some persistent debates are revisited (such as on the current status of the savanna hypothesis and on whether or not there was mammalian species' turnover in the Turkana Basin during the Plio-Pleistocene). The relation of hominin evolution to the recent finding of several turnover pulses coincident with global cooling trends in the 10 Ma to recent record of all African larger mammals is considered. One example of hypotheses which address issues of environmental stimuli of ontogenetic evolution is the heterochrony pulse hypothesis: the generative properties shared among lineages can result not only in coherence of morphological changes but also in a strongly nonrandom timing of heterochrony events, as diverse lineages respond in parallel by similar kinds of heterochrony to the same environmental changes. The discussion includes cases in hominins and other mammals of evolutionary increase in body size by prolongation of growth and attendant "shuffling" of body proportions including relative increase in brain volume, namely, encephalization.

Introduction

It is a truism that environmental stimuli have influenced the evolution of hominins and all other life forms. The challenge is to understand the causal subcategories: what are the hypotheses and predictions that should be tested and what kinds of data can be used to best effect. This approach is based on three premises: (1) one needs to study not only the hominins but also their wider biotic and environmental contexts. (2) Given the aim of understanding hominin evolution, the theory of evolution should be accorded more prominence than has been the norm, and an expanded theoretical framework is needed. A focus on the dynamics that link the environment to selection and adaptation at the organismal level is insufficient. One also needs to consider the causal linkages from the environment to dynamics at lower and higher levels – from morphogenesis during organismal ontogeny to the macroevolutionary level of species turnover (speciation and extinction) – and investigate the separate and combined roles in the origins of new phenotypes and species. (3) The direct influence of physical environmental stimuli on evolution at each level deserves more intensive study than it has been accorded traditionally. For much of the century following Darwin (1859), the research disciplines of geology (including climatology) and paleobiology were conducted separately. Speculations abounded on how they might link, but analyses directly integrating data from both areas remained sparse. This changed over the past decades as more refined methods led to discovery of new patterns and causal principles in paleoclimatology (e.g., the astronomical climatic cycles, Hays et al. 1976) and in the fossil record (e.g., rigorous phylogenetic hypotheses, geochemical inference of past diet, etc.). Proposals that hominins, the beginning of bipedalism, and other important human adaptations occurred in the African savanna, in response to the new selection pressures in such more open environments, are often loosely grouped under the term "savanna hypothesis." The first such proposal is often attributed to Dart (1925) who wrote (pp. 198–199), for example, that in the ancestral forest,

> Nature was supplying with profligate and lavish hand an easy and sluggish solution....For the production of man a different apprenticeship was needed to sharpen the wits and quicken the higher manifestations of intellect – a more open veldt country where competition was keener between swiftness and stealth, and where adroitness of thinking and movement played a preponderant role in the preservation of the species.

Later notable examples include the dietary hypotheses of Robinson (1963) and Jolly (1970). In his insightful review, Potts (1998b:107) considered that "Washburn's [1960 and other publications] influence and interest in intrinsic accounts (as opposed to extrinsic accounts, which interpreted evolutionary events in relation to environmental change) may explain why many paleoanthropologists in the 1950s–1970s paid little attention to environmental context." Early papers proposing physical change as a direct cause of hominin evolution concerned particular stratigraphic sequences in East and southern Africa (respectively, Coppens 1975; Vrba 1974, 1975; both compared climatic indications from mammalian change with the hominin record), the circum-Mediterranean area (Hsu et al. 1977 implicated the Messinian Salinity Crisis in hominin origin), and comparison of global climatic data with the hominin record (Brain 1981a).

Darwin (1859) argued that the initiating causes of phenotypic change and speciation are located at the level of organisms, namely, natural selection, particularly arising from competition: ".... each new species is produced . . . by having some advantage over those with which it comes into competition . . ." (p. 320). He stressed climatic effects on competition rather than on population structure: "in so far as climate chiefly acts in reducing food, it brings on the most severe struggle between the individuals...." (p. 68). Darwin thought that an understanding of organismal selection and adaptation will also answer the question of species' origins. Most later evolutionary studies, including those in paleoanthropology, have continued in this tradition. (See Tattersall 1997a who argued that "paleoanthropology fell completely under the sway of the evolutionary views of the [neoDarwinian] Synthesis – where it remains, for the most part, today.") The questions which will be addressed, using theory and evidence, include how physical dynamics have influenced species' structure and speciation, organismal ontogenetic systems, and selection and adaptation. I also consider some of the interactions among these levels.

Hominini means the evolutionary group of species which are considered by most to be more closely related to humans than to chimpanzees. The term "species" is used for a sexually reproducing lineage, the members of which share a common fertilization system, and "speciation" for the divergence of the fertilization system in a daughter population to reproductive isolation from the parent species

(Paterson 1982), with awareness of the difficulties involved in applying such concepts to the fossil record (Kimbel 1991; Vrba 1995a). The terms “habitat,” “specific habitat,” and “habitat specificity” of an organism or species refer to the set of resources that are necessary for life; resources are any components of the environment that can be used by an organism in its metabolism and activities, including ranges of temperature, relative humidity and water availability, substrate characteristics, places for living and sheltering, and all kinds of organic foods such as plants and prey, mates, and other mutualist organisms in the same or different species (Vrba 1992). An organism’s biotic environment derives from other organisms and biotic interactions such as competition, parasitism, predation, and mutualism. “Physical change” refers to the global and local effects from extraterrestrial sources, including the astronomical climatic cycles, and from dynamics in the earth’s crust and deeper layers as manifested by topographic changes such as rifting, uplift, sea level change, and volcanism. The use of the term “savanna” follows Ratnam et al. (2011) and Cerling et al. (2011:53): “a modern ecological definition of the term savannah is comprehensive and includes structural, functional and evolutionary aspects, Ratnam et al. 2011. Because our focus is on reconstructing the physiognomic structure of palaeo-vegetation, we use a purely structural definition of savannah [quoting Ratnam et al. 2011]: “mixed tree-grass systems characterized by a discontinuous tree canopy in a conspicuous grass layer.””

Physical Change, Adaptation, and Speciation: Some Current Hypotheses

The traditional hypothesis follows Darwin closely and has often been called neoDarwinian. In its most conservative form, it assumes that adaptation and speciation are always driven by natural selection. The particular causes of selection are seen as very diverse, the most important being organismal interactions – such as competition and predation – that can act alone, or in combination with physical change, to initiate and complete speciation (and extinction). Under this null hypothesis, H_0, selection pressures that cause speciation, differs from group to group and from one local area to the next. To explore how this model’s predictions differ from others, let us ask: what rhythm of speciation events would one expect if we could see all the events in the real world across the entire area under study (e.g., Africa) and if we plotted their frequencies against time? H_0 predicts that the pattern of origination frequencies for large areas, over long time, is a random walk in time with an averagely constant probability of origination. Examples of such arguments are found in Van Valen (1973), Hoffman (1989), McKee (1993), and Foley (1994). In contrast, a number of hypotheses share the argument that physical change has an important causal role in initiating the evolution of novel adaptations and species turnover, with the consequent prediction that such evolutionary events should be nonrandomly distributed in time and in association with episodes of physical change. Several such hypotheses will be discussed after introducing some relevant theory.

Allopatric Speciation

Allopatric speciation occurs in isolated populations that have been separated by vicariance or dispersal over barriers. (Vicariance is the fragmentation of a formerly continuous species' distribution into separated populations.) Gulick (1872), who studied the Hawaiian fauna, was the first to argue that the causes of speciation are not well explained by selection among competitors, but that vicariance brought about by physical changes was seminal in initiating speciation. Mayr's (1942, 1963) comprehensive arguments for allopatric speciation eventually resulted in widespread agreement that this mode predominates. Although there continue to appear claims of sympatric speciation, mainly in herbivorous insects and fishes, most recent such reports acknowledge that the best evidence remains circumstantial (review in Vrba 2005). It is fair to say that an expectation of predominant allopatric speciation, particularly in hominins and other large mammals, is consistent with the weight of available evidence and enjoys widespread consensus. In terms of earlier concepts of hominin phylogeny, which accepted a progression from the earliest biped to *Homo sapiens* with minimal branching from that lineage, one might wonder whether it is worthwhile to test causal hypotheses of hominin speciation, but recent finds indicate that "any accurate view of ourselves requires recognizing *Homo sapiens* as merely one more twig on a great branching bush of evolutionary experimentation" (Tattersall 1999:25, 2000). That is, we need to consider seriously the question of what caused lineage branching in the hominin tree.

Physical Change as the Driver of Vicariance, Selection, and Speciation

If allopatric speciation predominates, then so also must physical initiation of speciation predominate. Vicariance is nearly always produced by tectonic and climatic change. Incipient speciation initiated by dispersal over barriers also in most cases implies the causal influence of physical change (e.g., chance *Drosophila* fly dispersals over the ocean always occur, whether there are islands within reach or not; it took the production of the precursor islands of the Hawaiian Archipelago for the founding of those first allopatric populations of Hawaiian drosophilids, Carson et al. 1970). Thus, the chief causes of population size reduction and allopatry in the history of life have probably derived from physical changes. Although the relationship of punctuated equilibria to physical change was not explored in Eldredge and Gould (1972), the pattern they argued for implies independently that the initiation of speciation mostly comes about through physical change (Vrba 1980): if species are in equilibrium for most of their durations, what causal agency of the punctuation can one invoke other than physical change? The general consensus on the importance of allopatric speciation, together with the implications of punctuated equilibria and Paterson's (1978) "recognition concept" of species, led to the proposal that physical change is required for most speciation (Vrba 1980). Paterson (1978, 1982) argued that change in the fertilization system, the critical evolutionary change in sexual speciation, is most likely to occur in small, isolated populations that are under selection pressure from new environmental conditions.

Ecological Specialists and Generalists

This contrast is of general evolutionary interest (Stebbins 1950; Simpson 1953; Eldredge 1979; Vrba 1980, 1992) and particularly germane to mammalian evolution during the climatic instability of the late Neogene (Vrba 1987a). It has been discussed using various terminologies, such as stenotopy and eurytopy (e.g., Eldredge 1979), niche breadth (e.g., Futuyma 1979), and breadth of habitat specificity or resource use (Vrba 1987a). Specialist and generalist adaptation can be expressed in relation to different kinds of environmental variables, e.g., with respect to food intake, temperature, vegetation cover, light intensity, etc. Given the effects of the late Neogene climatic and tectonic changes in Africa (see sections "Physical Background: Climatic Change" and "Physical Background: Tectonism"), the distinction between species which are stenobiomic (restricted to a particular biome) and eurybiomic (ranging across biomes) is particularly relevant. As populations of a species encounter a new environment, beyond the ancestral biome range, they could in principle either diverge from their adaptation to the ancestral biome to become specialized on the new one or become more eurybiomic by broadening their resource use to include the new biome alongside the ancestral one (e.g., Vrba 1987a, 1989a). Evolution toward eurybiomy, which is very rare (e.g., Hernández Fernández and Vrba 2005 found a large preponderance of biome specialists in living African mammals), is of special interest as it applies to *Homo* (Vrba 1985a, 1989a; Pickford 1991; Potts 1998a; Wood and Strait 2003). Proposals that temporal and/or spatial environmental variability, namely, life in fluctuating or unpredictable environments, can promote generalist adaptations have a long history of extensive discussion (e.g., Stevens 1989 reviewed the evolution of broad climatic tolerance in high-latitude environments which have a greater range of annual and longer-term variation). Adaptations to strong seasonality range across life forms, from diatoms and other photosynthetic groups in polar waters (which each winter form resting spores in response to darkening and sink down dormant out of the plankton environment to germinate again when light returns, Kitchell et al. 1986) to the deciduous habit of many plants and hibernation and long-distance migration in animals. In advanced vertebrates, complex behaviors form an important category of such adaptations, ranging from the behavioral adjustments of animals to changing temperature and aridity (Maloyi 1972) to hominine culture.

The notion of a "biome generalist species" can be subdivided as follows. The eurybiomic phenotypes can be either (A) heritable, namely, genetically based and fixed, or (B) expressed as ecophenotypes, within a broad norm of reaction, in response to varying environments (Hall 2001; West-Eberhard 2003). Case (A) has two subcases. A1: Each organism can live in more than one biome, either because each organism has the needed biomic flexibility or because each organism is a specialist on resource patches which occur across biomes. An example of the latter is the aardvark, *Orycteropus afer*, which is stenophagous (it eats only ants and termites), a substrate specialist (it digs burrows in sandy or clay soil), and stenophotic (it is nocturnal). Yet *O. afer* is eurybiomic: its specialized "resource patches" range from semidesert to dense, moist woodland across Africa. A2: There are intraspecific differences in resource use among organisms and populations; i.e., polymorphism in resource use allows the species to respond to environmental fluctuations by shifting relative abundances of the variants. An example is the African buffalo (Sinclair 1977): *Syncerus caffer caffer* differs in phenotype and resource use from (and lives at higher latitudes and/or altitudes with more grassland present than) the smaller, plesiomorphic phenotype *S. c. nanus* (in warm, forested regions). This species appears to have "rolled with the punches" of large and frequent climatic changes since the late Pliocene mainly by changes in polymorphic frequencies. All generalist adaptations first evolve in populations, thus rendering the species polymorphic. Intraspecific adaptations and polymorphisms, which become more elaborate with repeated climatic shifting, are likely to be the most frequent responses to climatic extremes (see Vrba 1992: Fig. 4c) with speciation and extinction being rarer outcomes.

Habitat Theory and the Turnover-Pulse Hypothesis

The turnover-pulse hypothesis is a part of the broader "habitat theory" which focuses on species' habitats and on the dynamic relationships between physical change, habitats, and species (Vrba 1985b, 1992). It uses the predominance of allopatric speciation and the consequence that physical change is required for most speciation. Climatic changes (from global or/and local tectonic sources) result in removal of resources from parts of the species' former geographic distributions and therefore in vicariance. Vicariance on its own is insufficient for speciation. Many species underwent repeated episodes of geographic shifting, vicariance, and reunion of their distributions in response to the astronomical climatic oscillations, without speciation although intraspecific adaptive changes may have accumulated (Vrba 1992, 2005). For speciation to occur, physical change must be strong enough to produce population isolation, but not so severe as to result in extinction, and the isolated phase must be of sufficiently long duration for the changes which define speciation (divergence of the fertilization system) to occur. It has been suggested that most speciation requires sustained isolation or near isolation, without rapid reintegration on the Milankovitch timescale, and that shrinking populations are important in which habitat resources are dwindling and competition increases, with consequent strong selection from the changing environment (Vrba 1995b). In the absence of physical change of appropriate kind and duration, although species may accumulate new adaptations, they are buffered against speciation at several levels (review in Vrba 2005).

One prediction is that most lineage turnover, speciation and extinction, has occurred in pulses, varying from tiny to massive in scale, across disparate groups of organisms, and in predictable temporal association with changes in the physical environment (Vrba 1985b, 2005). If we think of origination, several possible patterns of origination frequency could result, all different from the temporally random pattern predicted under H_0: (1) origination could in principle be confined to rare, large pulses in response to the largest environmental changes. Such large pulses may resemble jagged mountain crests, or dissected high plateaus, rather than simple, single peaks because the timing of turnover responses to climatic or tectonic episodes will differ among organismal groups and local areas. (2) Many, frequent, small pulses, such as in response to the 100 Ka astronomical cycle, interspersed by the less frequent, larger ones described under (1). (3) Combinations of the random null model and the turnover-pulse hypothesis suggest additional predictions such as a random background of turnover frequency punctuated by rare pulses. A comparison among turnover pulses is expected to show much heterogeneity – or "mosaic" differences. The environmental changes that trigger turnover are diverse. They vary in nature, intensity, timing – how long they endure, how much fluctuation occurs, and steepness of component changes and net trends – and in geographic emphasis and extent, from very localized to present in many parts of the earth. Topographic and latitudinal factors contribute to geographic variation in the turnover responses to a major global change. Also, the different organismal groups differ sharply in how they are affected by climatic variables (see Andrews and O'Brien 2000 for mammals). They differ in response (by speciation, extinction, intraspecific evolution, or no response at all). Lineages which do undergo turnover initiated by a given physical change may do so with different timing (in "relays," see examples in Vrba 1995b, 1995c). Thus if a turnover pulse is detected in a data set, it is desirable to study subdivisions of those data to understand the detailed taxonomic, geographic, and temporal patterns.

Additional hypotheses: (1) Under habitat theory and other concepts which invoke predominant allopatric speciation, the species should generally "start small," namely, in geographic distributions that are more restricted than those they attain later on (Vrba and DeGusta 2004). H_0 does not predict this. (2) Of two areas of similar large size, both subject over the same time to climatic cyclic extremes that remain habitable for organisms; the area that is more diverse in topography will have higher incidences of selection pressures and vicariance per species. The prediction is that the topographically more diverse area has higher rates of vicariance, speciation, and extinction (Vrba 1992). (3) During periods of strong latitudinal thermal contrasts, with ice caps on one or both poles, biomes closest to the equator are predicted to have higher speciation and extinction rates than biomes at adjacent, higher latitudes (e.g., this bias may have contributed to the high species richness in the tropics today, Vrba 1985b, 1992.). (4) Biome generalists are expected to have lower rates of vicariance, speciation, and extinction than biome specialists (Vrba 1980, 1987a, 1992). Because habitat theory stresses physically initiated vicariance and selection pressure, changes in amplitude and mean of the climatic cycles, and in which cycle predominates, are expected to affect the evolutionary outcome. The larger the amplitude, the higher the incidence of vicariance and selection pressure at any cyclic extreme, accelerating the rates of intraspecific adaptation, speciation, and extinction. Changes in cyclic dominance can affect the frequency and duration of vicariance. Large translations in the climatic mean and envelope may be especially significant for speciation and extinction (Vrba 1995b: Figs. 3.2, 3.3).

The Coordinated Stasis Hypothesis

Brett and Baird's (1995) hypothesis of coordinated stasis is Darwinian in a focus on organismal interactions in a community as a source of stasis. It proposes that the coevolutionary bonds during stasis are so strong that physical change is needed to disrupt them to result in turnover. Thus this model is "community based" in its theoretical assumptions (see also the hypothesis of coevolutionary disequilibrium of Graham and Lundelius 1984 and reviews in Barnosky 2001; Vrba 2005). Brett and Baird's (1995) model predicts stasis of species, interrupted by pulses of speciation and extinction, across all communities in which a set of species occurs. Thus, their predictions are closely comparable with those of the turnover-pulse hypothesis, as acknowledged by Brett and Baird (1995:287): "The same term [coordinated stasis] could be used for the blocks of stability in Vrba's (1985b) 'stability-pulse' hypothesis."

The Variability Selection Hypothesis

This hypothesis was proposed and applied to hominin evolution by Potts (1998a, 1998b, 2012; pages quoted are from the 1998a paper unless otherwise noted). It is about (1) a particular category of adaptations which he calls "variability selection adaptations" (VSAs), (2) their initial appearance and establishment, (3) their fate in the face of long-term climatic cycles, and (4) an interpretation of the theoretical implications of their evolution:

1. VSAs are "structures and behaviors responsive to complex environmental change" (p. 81), which are uniform within species "yet able to mediate secondary phenotypic traits that vary…" (p. 85). His examples include a locomotor system allowing a wide repertoire of movement and "a large brain or specific neurological structure that is effective in processing external data and generating complex cognitive responses" (p. 85).
2. VSAs arise first in isolated populations. Intraspecific polymorphism results with VSAs in some populations and not in others. Organismal selection from short-term variability during organismal lifetimes initially promotes such VSAs (or at least allows them to persist).
3. The long-term evolutionary outcome at Milankovitch and longer timescales is that organisms with VSAs survive climatic extremes. Therefore species, which include at least one VSA-carrying population, survive. Over time the VSAs can become more elaborate as climatic extremes recur. Thus, high climatic amplitude at timescales longer than organismal life times, notably at Milankovitch and longer timescales, causally influences the evolutionary outcome.

4. Climatic variability at the longer timescales is a selective agent of VSAs, which are "designed [by selection] to respond to novel and unpredictable adaptive settings" (p. 85). That is, these organismal adaptations are shaped by selection for the function of flexible responses to future climatic excursions of the Milankovitch cycles, and this is a new kind of selection: "variability selection" (VS).

Potts regards his concept as distinct from previous concepts, notably from the (p. 82) "savanna hypothesis" and other "environmental hypotheses of hominin evolution [which focused] on a specific type of habitat." Proposals (1), (2), and (3) are severally and jointly consistent with previous theoretical proposals (see section "Ecological Specialists and Generalists"). The sole departure is proposal (4) of a distinct type of selection, which is commented on next.

The special effects which the high amplitude of climatic cycles since the late Pliocene had on the biota (e.g., that species, in which generalist adaptations for climatic tolerance evolved, survived disproportionately) has been much discussed (e.g., Stanley 1985; Vrba 1985a, 1992, 2000). No one doubts that strong Milankovitch excursions can selectively remove some populations and species whose organisms are unfit under those conditions, nor that generalist adaptations of survivors can sequentially be elaborated during recurrent such episodes. But this would not be a new kind of selection. *Organismal selection* cannot promote adaptations to future Milankovitch extremes, although *inter-demic selection* (Wright 1932, 1967) or *species selection* (review in Vrba 1989b) could in principle occur at those longer timescales. (In fact, Potts did at one stage wonder whether his notion might represent a form of lineage or species selection, R. Potts pers. comm.). The problem is that the concept of selection and adaptation at levels higher than that of organisms is onerous (Williams 1966; Maynard Smith 1987; Vrba and Gould 1986; Vrba 1989b). Maynard Smith (1987) discussed this as follows (p. 121): "We are asking whether there are entities other than [organisms] with the properties of multiplication, heredity, and variation, and that therefore evolve adaptations by natural selection." Considering the nature of the adaptations Potts (1998a) had in mind, one probably does not need to invoke higher level selection. Such issues on levels of selection have been extensively debated and with respect to diverse organismal case histories. An example which is of interest here, in spite of (and perhaps because of) being far removed from hominins on the tree of life, is the case in diatoms of the resting stage adaptation to polar conditions of long winter darkness (Kitchell et al. 1986): The fossil record shows that diatoms living in Arctic waters just before the Cretaceous/Tertiary (K/T) boundary already had this life cycle adaptation. Kitchell et al. (1986) documented that during the K/T mass extinction (which involved long-term global darkening), diatoms and other photosynthetic planktonic groups with resting stages had markedly lower extinction rates than groups which lacked this seasonal adaptation. They argued (correctly in my view) that these life history features, which arose by selection at the organismal level as adaptations to seasonal variability, were also fortuitously (by sheer luck) available and useful during the K/T event for weathering much longer intervals of darkness. They concluded that this sorting among species, although nonrandom, does not represent species selection but species sorting according to the effect hypothesis (Vrba 1980). The adaptation is this case could not have been selected at the organismal level for climatic variability at the timescale of mass extinction. The selective forces and character complexes which contributed to the survival of hominins and other mammals in the face of increasing climatic amplitude during the late Neogene may in principle fall into the same category.

Additional Comments on Environmental Hypotheses of Hominin Evolution

In the current spirited and exciting debate on the various hypotheses (savanna, variability selection, turnover pulse, habitat theory, and more), some confusion has crept in, which is affecting the debate in a negative way to the point where sometimes the discussants are talking past each other. While Potts (2012:154) wrote that "Regarding the external drivers of human evolution, the primary alternative to Vrba's TPH [turnover pulse hypothesis] has been the variability selection hypothesis," the points raised here are relevant to all the hypotheses and all parts of the debate. Three such issues will be mentioned here.

1. **Specific Habitats, Species-Specific Habitats, and Other Specific Notions.** Consider these quotations: "The VS [variability selection] hypothesis differs from prior views of hominin evolution, which stress the consistent selective effects associated with specific habitats or directional trends (e.g., woodland, savanna expansion, cooling)" Potts (1998a:81). "Habitat-specific adaptations may entail a more limited responsiveness to environmental perturbation..." (Potts 1998a:155). "Over the past three decades, the environmental study of human evolution has been dominated by the search for the preferred [i.e., specific] habitat of each hominin species. This approach has led to a far more static concept of early hominin adaptation..." (Potts 1998a:161). This pits "consistent selective effects," "specific habitats" and "habitat-specific adaptations" of "limited responsiveness," and directional climatic trends (the not-so-good "static concept") against variable selective effects, variable habitats, and "variability selection adaptations" and pervasive climatic oscillations and environmental complexity (the good, dynamic concept). But is this a substantive dichotomy with correct characterization of both sides? It is not, and one "culprit" is the interpretation of the word "specific."

   In the present context, "specific" simply means "relating to, characterizing, or distinguishing a species," thus neutral on breadth and changeability of adaptation, habitat, or environment in this case. The definition of the specific habitat of a species (see third paragraph in introduction of this review, which describes how many including the present author have used it) is indeed neutral on degree of variability, referring only to a list of resources and their ranges which describes where and how the species can live. In principle, the resource ranges of the specific habitat can be extremely broad. Consider an extreme and hypothetical example of a land species which can live everywhere within a temperature range of 0–100 °C. Its specific habitat with respect to temperature is the range 0–100 °C. A related point: the notion that each species is "specific for a particular *habitat*" does not equate with specificity for a particular – or single – type of *environment*. For example, the aardvark, while a specialist in terms of food and substrate, ranges widely across Africa from semidesert to dense, moist woodland. A species' habitat may remain intact although it lives in strongly fluctuating environments over long time, such as the aardvark whose habitat and resources persisted as widely varying environments swept over the areas in which it lived. In other cases, habitat variability – such as variable use of food and substrate – is an integral part of the habitat specificity of the species (see 2).

Unfortunately, such simple misunderstandings can spread and eventually harden. For example, deMenocal (2004:4) stated that "most environmental hypotheses of African faunal evolution are 'habitat-specific' (Potts 1998b) in that they consider faunal adaptations to a specific environment, most commonly the emergence of grassland savannah…"

2. **Adaptation to Variability.** Potts (1998a, 1998b, 2012) regards the VSA (variability selection adaptation) concept as distinct from previous concepts of adaptation, such as the generalist adaptations which confer eurytopy (Eldredge 1979), broad habitat specificity (Vrba 1987a), and broad climatic tolerance (Stevens 1989). He considers "habitat-specific" adaptations (e.g., Vrba 1987a) and selection pressures as different from VSAs and VS because the former in his view narrowly refer to a particular kind of environment and not to variable environments. He is wrong in these claims.

   Structures and behaviors that confer flexibility in the face of – and are usually ecophenotypic or genetically based adaptations to – climatic variations, and that may arise and exist as polymorphic variants in species, are well known (e.g., the resting/vegetative life cycle in diatoms noted above, hibernation, etc.) including complex behaviors in primates (e.g., the presence in some Japanese macaque populations of grass-washing behavior, Nakamishi et al. 1998). Concerning human evolution, as reviewed below, many have written about adaptation to variability (including environmental heterogeneity at any one time) and the effects of climatic cycles. As Potts (2012:154) considers habitat theory and the VS hypothesis as "primary alternatives," any impression that previous discussions of human evolution in the light of habitat theory (e.g., Vrba 1985a, 1989a) have ignored hominin adaptation to climatic variability needs to be corrected. One hypothesis (Vrba 1989a:30) concerns culture in general:

   > *The culture of the genus* Homo *is a generalist adaptation*. Hominine culture is an extension of the common phenomenon in other animals that use behaviour to cope with climatic conditions. … a special case among animal behaviors that confers an expanded use of environmental resources. In contrast, robust australopithecines were more specialized on open, arid habitats.…[and in *Homo* occurred] a switch to the crucial generalist adaptations of brain and culture that have made us the least environment-dependent species on earth today.

It turns out that Vrba's (1989a) hypothesis that the robust australopithecines "were more specialized on open, arid habitats" is probably wrong (see review below). However, it now seems likely that the masticatory features of *Paranthropus*, while adaptations for consuming tough or gritty foods, had the effect of broadening, not narrowing, the range of food items consumed and allowed these forms to subsist in varied environments (Wood and Strait 2003).

One hypothesis on hominin adaptation to climatic variability, which is plausible and deserving of testing, is that humans descend from deep nomadic (migratory) ancestry, at least since the onset of advanced bipedalism in *Homo* ca. 1.6 Ma, which falls during a time of change to more open and seasonally arid landscapes:

> As Baker (1978) observed, most animals are 'migratory' to some extent. But it is undeniable that those living in open, arid habitats, where resources tend to be patchy in space and/or time, invariably have a greater tendency to seasonal and more extensive movement... Did one or both of the hominin lineages that diverged during the Pliocene migrate seasonally across ecotonal margins? (Vrba 1985a:70).

If evidence of hominid nomadism in the Early Pleistocene were to be found (as it might be, for instance, by isotopic analysis of diet in conspecific hominins), one would still need to ask whether that nomadic potential was there previously or whether it evolved de novo by genetically based broadening of the norm of reaction to allow both nonmigratory and migratory behavior depending on seasonality. If the latter is true, then migratory behavior by *Homo* could surely be termed a good habitat-specific adaptation and a good variability selection adaptation. The use of different wording does not change the logic of that.

3. **Climatic Variability.** Potts (1998a, 1998b, 2012) concluded that others with versions of the savanna hypothesis that were articulated previous to his VS hypothesis, which includes me, were focusing narrowly on long-term cooling trends and failed to incorporate observations about patterns of African paleoclimatic variability from deep-sea cores and recently also from coring on the African continent (Scholz et al. 2007; Cohen et al. 2007; reviewed below). Again, the issue must be taken with this. First of all, the focus on long-term trends (e.g., Vrba 1995b) is a necessary part of the study of climatic variability in mammalian evolution: the shorter-period Milankovitch cycles modulate each other which gives rise to cycles of longer periods (and therefore to long-term cooling and warming trends) which are associated with ice sheet expansion and cooling and turn out to be important triggers of mammalian speciation and extinction (e.g., cycles with periods of ca. 1 Ma and ca. 2.4–2.5 Ma; see van Dam et al. 2006). More generally, it was the realization of the potentially enormous implications of the climatic oscillations for evolution of new form, function, and species in hominins and other mammals – of the fact that the "species specific for these . . . biomes are riding along on their 'habitat plates', that drift back and forth rapidly . . . over the tectonic plates that drift more slowly beneath" (Vrba 1992:11) – that prompted the organization of an interdisciplinary conference to explore those implications (Vrba et al. 1995). It was argued then

(Vrba 1995a:33) that "if prolonged vicariance is important for turnover and especially for speciation, then major shifts in the *mode*, or periodicity pattern, of the astronomical cycles should be examined for associated turnover" (see also Vrba 1992), and a model was illustrated (Vrba 1995a:30–33), using Shackleton's (1995: Fig. 17.3) data which records delta^{18}O variation at 0.003 Ma interval steps for the past 6 Ma, for measuring climatic variability. Because this way of measuring climatic variability monitors the outer envelope of climate curves step by small step, it is expected to detect major changes in climatic mode such as documented by deMenocal and Bloemendal (1995): a shift from dominant climatic influence occurring at 23–19 Ka periodicity prior to ca. 2.8 Ma to one at 41 Ka variance thereafter, with further increases in 100 Ka variance after 0.9 Ma (see also Ruddiman and Raymo 1988). (Some results will be compared in section "Physical Background: Climatic Change" with those of others who have measured variability in climatic curves, including Potts 1998a.)

In sum, how do the turnover-pulse hypothesis (within in more general habitat theory which includes responses to climatic variability of generalists and specialists) and the variability hypothesis compare in terms of content? Readers will make up their own minds. My conclusion is that they do not differ substantively in terms of the basic processes implied. There are differences in emphasis, in terms used, and in how the terms they have in common are interpreted (particularly the term "specific habitat" of species).

Is the early savanna hypothesis still alive and well? Yes, the basic hypothesis – that climatic change has caused reductions in wood: grass cover proportions which affected hominin populations and evolution – remains a good one, although it has evolved and branched out into more sophisticated versions. Cerling et al. (2011) showed that the fraction of woody cover in tropical ecosystems can be quantified using stable carbon isotopes in soils and applied the method to fossil soils from hominin sites in the Awash and Omo-Turkana basins. They concluded (p. 55) that "the combined results from two of the most significant hominid-bearing regions in eastern Africa leave the savanna hypothesis as a viable scenario for explaining the context of earliest bipedalism, as well as potentially later evolutionary innovations within the hominin clade."

Tests Based on the Temporal Distribution of Newly Appearing Phenotypes and Species

The models above all predict significant concentration in time of particular newly appearing morphologies and in the case of the coordinated stasis and turnover-pulse hypotheses also of speciation and extinction events. All of them predict that such events in the fossil record should associate significantly with climatic change. Most difficulties in testing such hypotheses have to do with errors in the chronological, physical, and biotic data and with testing at inappropriate temporal, geographic, and taxonomic scales (Barnosky 2001). There are two types of errors in such tests:

inferring fossil events that are not there (i.e., erroneous rejection of H_0, Type I error) and failure to detect real events (Type II error) as exemplified by Signor and Lipps (1982). Take, for example, a Type II error under the turnover-pulse or coordinated stasis hypotheses, the attempt to distinguish between H_0, and real small speciation pulses that occurred at the Milankovitch timescale. Such a test using first appearance data with lower time resolution (e.g., the data for 0.5 Ma-long intervals length in Vrba and DeGusta's 2004 study of African mammals) will fail, although major pulses might be detectable. The main bias that leads to Type I error, seeing pulses that are not there, arises from unequal fossil preservation between time intervals, areas, and groups of organisms, the "gap bias" (Vrba 2005): any given species' fossil FAD (first appearance datum) may postdate its true, or cladistic, FAD (Kimbel 1995). Gaps have the effect that, for instance, a count of FADs in an interval is erroneously inflated by FADs of species which in reality originated (but were not detected) previously. An early version of a test that corrects for the "gap bias," thus allowing a rigorous test of the pulse hypothesis, was applied to the African larger mammals of the past 20 Ma divided into 1 Ma-long intervals (Vrba 2000). More recently, a second, updated form was applied to the nearly 500 African species recorded over the past 10 Ma divided into 0.5 Ma-long intervals (Vrba and DeGusta 2004; Vrba 2005). Time resolution in this record is sufficiently good, with more than 70 % of the site records dated by radiometric or paleomagnetic means, that any large speciation (or extinction) pulses spaced sufficiently far apart in time should be detectable. Some results will be mentioned in section "The Record of First Appearances of Mammalian Species."

Physical Change, Adaptation, Speciation: Evidence from the African Neogene

Physical Background: Climatic Change

Following the definitive documentation of the astronomical cycles (Hays et al. 1976), it was thought that they may have had little effect on the tropics in general (review in Burckle 1995) and on African hominin-associated environments in particular. For example, Hill (1995:187) considered that "it may be that African terrestrial vertebrate habitats were to some extent buffered from climatic changes seen elsewhere." Hill's caution is well taken that specific areas may "march to a local drummer" especially if that drumbeat derives from tectogenesis (see below). It now appears that much of Africa participated in global as well as more localized climatic changes over the time period of interest, namely, the late Miocene-Recent record, as the earliest hominin fossils currently date to ca.7 Ma ago (Brunet et al. 2004). For much of this time Africa has been influenced by two separate processes (deMenocal 2011): forcing from the orbital precession cycle has brought about monsoonal cycles that alternated between wet and dry conditions, and superimposed on these was a long-term trend toward increasingly more arid and more variable conditions.

The Late Miocene. Changes in polar ice volume and sea level have greatly influenced African climate and human evolution as cited variously below. By the time hominins evolved, there had been large ice sheets in Antarctica since 33 Ma (following a previous time of ephemeral ice sheets), while the earliest extensive Arctic glaciation was established much later, by 2.7 Ma and contemporaneously with the first appearance of *Paranthropus*, the robust australopithecines, and probably also of the lineage to modern humans. Miller et al. (2005) discussed the relations of ice sheets, global climate, and sea level and considered that sea level mirrors oxygen isotope variations, reflecting ice-volume change and thus global climate on the 10,000 year–1,000,000 year timescale which applies to human evolution. They found prominent sea level falls and thus global climatic events, at 8.2 Ma, 5.7 Ma, 4.9 Ma, 4.0 Ma, 3.3 Ma, and 2.5 Ma. There was ice buildup on West Antarctica and general increase in delta^{18}O values 7.0–5.0 Ma ago (Kennett 1995). A major cooling which started before 6 Ma and peaked shortly thereafter contributed to isolation and desiccation of the Mediterranean Basin during the Messinian low-sea level event and salinity crisis dated ca. 5.8–5.3 Ma (Haq et al. 1980; Hodell et al. 1994; Bernor and Lipscomb 1995; Aifa et al. 2003; Garcia et al. 2004). This major cooling coincides with a strong vegetation change ca. 6.3–6 Ma, with a large decrease in tree cover and increased aridity in both West and East Africa, according to Bonnefille's (2010) overview of macrobotanical (fossil wood, leaves, and fruits) and microbotanical (mainly pollen) evidence for the past 10 Ma in tropical Africa with special reference to the hominin sites. After the Messinian followed warming and a transgressive phase started before 5 Ma and reached a maximum in the 5–4 Ma interval, according to Haq et al. (1987).

Questions remain on the African effects of these late Miocene climatic events. Kingston et al. (1994) found that, in the Kenyan Tugen Hills area, a heterogeneous environment with a mix of C_3 and C_4 plants – and without grassland dominance – persisted over the entire past 15 Ma without any apparent local influence from global climatic change. Yet evidence from Lothagam indicates that this part of Kenya experienced strong environmental changes over the latest Miocene (Leakey et al. 1996; Leakey and Harris 2003). Further evidence comes from analyses of carbon isotope ratios in soils and fossil tooth enamel. Cerling et al. (1997) studied fossil herbivores ranging over the past 22 Ma from several continents. Using the fact that low delta^{13}C values in herbivore teeth reflect a diet of mainly C_3 plants, while high values indicate feeding on C_4 plants, they found that up to 8 Ma ago, mammals in Pakistan, Africa, and South and North America had C_3 diets or C_3-dominated diets. By the late to latest Miocene, C_4 plants came to dominate the diets. In Kenya, representing the lowest latitude in the sample, the transition was complete by between 8 and 6.5 Ma and in Pakistan by ca. 5 Ma. Cerling et al. (1997) interpreted their results as showing a global increase in the biomass of C_4 plants 8–6 Ma ago which resulted from a decrease in atmospheric CO_2.

The Plio-Pleistocene. Interest in African hominin-associated climatic changes has burgeoned greatly over the past decade. Here, only a few examples are given from the large volume of evidence for the Plio-Pleistocene, from research on broader regional climatic variability, to illustrate some of the basic lines of enquiry and the diversity of approaches. Additional evidence more directly focused on hominin environments will follow below. Clemens et al. (1996) discussed how monsoon variability and evolution respond to external forcing (orbitally driven changes in solar radiation) and internal forcing (interaction among the atmosphere, oceans, land surface, and ice sheets). They examined a deep-sea sediment record spanning the past 3.5 Ma from the northwest Arabian Sea and compared diverse proxies, including abundances of *Globigerina bulloides*, biogenic opal content which indicates radiolaria and diatom production, and lithogenic grain size of the deep-sea sediments, all of which in this area can indicate the strength of the Asian monsoon. Clemens et al. (1996) argued that the growth of Northern Hemisphere ice sheets over the past 3.5 Ma weakened the Asian summer monsoon and increased the aridity of subtropical Asia and eastern Africa. They demonstrated that the phase relationships between the African monsoon and the glacial cycles were shifting continuously over the past 2.6 Ma, explaining why indicators of surface water such as lake levels and of vegetation, such as dust spikes, often do not covary. The authors found significant shifts in the intensity and phase of the Indian monsoon at ca. 2.6 Ma, 1.7 Ma, 1.2 Ma, and 0.6 Ma. deMenocal (2008, 2011:541) discussed the large amplitude of the African wet-dry monsoon cycles using the example of changes in the Sahara and pointed out the usefulness of sapropel layers as proxies (see also Rossignol-Strick 1985; Rossignol-Strick et al. 1998) for detecting the intensity and phase of the monsoon cycles:

> From 15,000 to 5,000 years ago, the modern Saharan Desert was nearly completely vegetated, with large, permanent lakes and abundant fauna. Precessional increases in summer radiation invigorated the monsoon, delivering more rainfall deeper into Africa, and enhanced Nile river runoff flooded into the eastern Mediterranean Sea. The resulting freshwater stratification created anoxic conditions and led to deposition of organic-rich sediments (sapropels) on the seafloor.

Similarly, Cole et al. (2009, 2012) found evidence for the prevalence of extensive paleolakes in the Sahara during the African humid period.

The opposite extreme, “megadrought,” has also been documented. In companion papers, Scholz et al. (2007) and Cohen et al. (2007) presented results from drill cores from Lake Malawi and point out that by 2007, these were the first long and continuous, high-fidelity records of tropical climate change from the African continent itself. Their record documents periods of severe aridity between 135 Ka and 75 Ka ago, when the lake’s water volume was reduced by at least 95 %. Scholz et al. (2007:16416) wrote, “Surprisingly, these intervals of pronounced tropical African aridity in the early late-Pleistocene were much more severe than the Last Glacial Maximum, the period previously recognized as one of the most arid of the Quaternary.” According to Cohen et al. (2007:16422), “Fossil and sedimentological data show that Lake Malawi itself, currently 706 m deep, was reduced to a ca. 125 m deep saline, alkaline, well mixed lake.”

Among Plio-Pleistocene records that demonstrate the large effects of global climatic change on Africa, many are based on signatures from plants, algae, or other indicators of overall plant cover such as dust. Pollen cores off West Africa record the shifting of the Sahara-Sahel boundary and the earliest extensive spread of the Sahara desert ca. 2.8–2.7 Ma ago (Dupont and Leroy 1995). One of the two strongest vegetation changes found by Bonnefille (2010) across tropical Africa over the past 10 Ma occurred at 2.7 Ma (p. 391): "abrupt decline of forest pollen accompanied by an increase in grass pollen was found at 2.7 Ma, . . . accompanied by a significant increase in C-4 grass proportions, well indicated in the Turkana region and likely explained by an increase in dry season length." Marlow et al. (2000) used an index based on the ratio of two types of alkenones (chemical compounds produced by specific species of haptophyte algae) to measure sea surface temperature (SST) in a marine core off Namibia. They presented their continuous time series of changing SST for the past 4.5 Ma, as well as estimates of paleoproductivity from the mass accumulation rates of organic carbon, diatom abundances, and diatom assemblages. Marlow et al. (2000) interpreted decreased upwelling to represent warmer conditions with wetter, more mesic periods in southern Africa and concluded that SSTs decreased markedly, in association with intensified Benguela upwelling, after 3.2 Ma, with subsequent periods of marked SST decrease and upwelling intensification near 2.0 Ma and 0.6 Ma. Another marine record from southwestern Africa, off Angola, derived from carbon isotope analyses of wind-transported terrigenous plant waxes, indicated African C_4 plant abundances 1.2–0.45 Ma (Schefuss et al. 2003). The evidence showed that the African vegetation changes are linked to SST in the tropical Atlantic Ocean and that changes in atmospheric moisture content due to tropical SST changes and the strength of the African monsoon controlled African aridity and vegetation changes. Marine records off West Africa and from the Gulf of Aden have documented delta^{18}O variations and also dust influxes from the Sahara and Sahel regions in the West and from Arabian and northeastern African areas in the Gulf of Aden (deMenocal and Bloemendal 1995; deMenocal 2004). The latter paper reported steplike shifts in the amplitude and period of eolian variability at 2.8 (±0.2) Ma, 1.7 (±0.1) Ma, and 1.0 (±0.2) Ma.

As one method to use climatic records to predict over which time intervals vicariance (population fragmentation) should be particularly concentrated, the following hypothesis was introduced with discussion on how to test it: "*long-term, continuous vicariance*, and long-term increases and decreases in the minimum- and maximum-value envelopes of the astronomical climatic cycles, are the kinds of allopatry and climatic change that are particularly important for speciation" (Vrba 1995b:27 and following pages). Shackleton's (1995: Fig. 17.3) data were used, which record delta^{18}O variation at 0.003 Ma interval steps for the past 6 Ma, to identify periods over which the largest net cooling or warming trends occurred. (Vrba 2004: take an interval t_x of length x Ka, for example, t_{100} for $x = 100$ Ka, and move it step by step along the time axis from early to late. At each interval step, mark the interval along the time axis if either of conditions C, for cooling, or W, for warming, is true. C: the upper [warm] envelope of the climatic curve remained continuously below the running mean of the previous 300 Ka, i.e., the interval is a $t_{100,C}$, or an interval of length 100 Ka with marked cooling. W is the corresponding condition for a warming trend. A pattern of $t_{100,C}$ and $t_{100,W}$ distribution in time results, with data clusters for the most sustained trends. I here report results for separate assessments using interval lengths in Ka of x = 40, 65, 100, and 140.) The following approximate intervals (in chronological sequence) emerged as times of sustained net cooling ($t_{40,C}$, $t_{65,C}$, $t_{100,C}$, and $t_{140,C}$ are respectively labelled as *, **, ***, and ****, from least to most severe; time ranges in ca. Ma): 6–5.7****, 5.1–4.9*, 4.2–3.9*, 3.4–3.2***, 2.9–2.3 especially 2.7–2.5****, 2.1–2.0*, 1.8–1.65**, 0.95–0.85**, and 0.8–0.65** (and 0.8–0.6*). Intervals of net warming (similar notation as for cooling): 5.6–5.35****, 4.5–4.4*, 3.1–2.9*, 1.65–1.6*, and 0.85*. Because this method of measuring changes in climatic variability, in this case in delta^{18}O variability, monitors the outer envelope step by small step, it is expected to detect major changes in climatic mode such as documented by deMenocal and Bloemendal (1995): a shift from dominant climatic influence occurring at 23–19 Ka periodicity prior to ca. 2.8 Ma to one at 41 Ka variance thereafter, with further increases in 100 Ka variance after 0.9 Ma (see also Ruddiman and Raymo 1988). Comparison with the results in the previous paragraph shows that this way of measuring change does succeed in detecting the major dominance shifts. There are now several such approaches. For example, Potts (1998a) subtracted the lowest from highest value for each unit million year as a measure of total climatic variability for that unit year. He found that variation of 0.3–0.5 parts per million (ppm) is obtained for most of the Neogene until the 6.0–5.0 Ma interval, during which variability rose sharply. After a minor decrease during 5 to 4 Ma, there were increases during every succeeding interval with the highest one, to 1.9 ppm, during the past 1 Ma (Potts 1998a:83, Fig. 1). Donges et al. (2011) applied a nonlinear method of time series analysis, recurrence network, to records of dust flux. They found (p. 20422) three "transitions between qualitatively different types of environmental variability in North and East Africa during the (i) Middle Pliocene (3.35–3.15 Ma B. P.), (ii) Early Pleistocene (2.25–1.6 Ma B. P.), and (iii) Middle Pleistocene (1.1–0.7 Ma B. P.)," which approximately also appear among my results, as does the mode change 6.0–5.0 Ma ago found by Potts (1998a).

It is worth noting the major climatic changes, including some with rough consensus on when they occurred, from the diverse sources cited above: 8.2 Ma, 7–6 Ma, and associated with the Messinian ca. 5.8–5.3 Ma, ca. 5 Ma, 4.2–3.9 Ma, 3.5–3.2 Ma, 2.9–2.3 Ma, 1.8–1.6 Ma, 1.2 Ma, and 1.0–0.6 Ma.

Physical Background: Tectonism

Tectogenesis has featured less prominently than climate change in discussions of evolution, perhaps because it is mostly a slow process and the date limits for events tend to be wide. Yet it has had a primary influence on landscape and biotic evolution. This includes hominin evolution especially in rift-associated environments as recognized long ago by Coppens (1988–1989). Crustal changes influenced climate on a grand scale, e.g., the late Pliocene closure of the Isthmus of Panama may have led to the start of the modern ice age (Maier-Reimer et al. 1990; Haug et al. 2001). The uplift of western North America, the Himalayas, and the Tibetan

Plateau possibly influenced the Pleistocene cooling intensification ca. 1 Ma ago (Ruddiman et al. 1986). Northward drift of Africa during the Neogene led to southward displacement and areal decrease of tropical African forests and contributed to long-term aridification (Brown 1995). Episodes of intensified African uplift since ca. 30 Ma ago, which raised the entire eastern surface higher than in the West, greatly affected the African climate (Burke 1996). Apart from the numerous localized climatic effects of tectogenesis (e.g., Feibel 1997), the *topographic diversity* it generates *together with the superimposed climatic cycles* constitutes a prime cause of spatial and temporal environmental heterogeneity, changing selection pressures, and speciation (Vrba 1992). Thus evolution of the African Rift had an especial role in some evolutionary events in hominins (Coppens 1988–1989) and other mammals (e.g., Denys et al. 1987). The present episode of rifting began in the Early Miocene (Frostick et al. 1986). Ca. 8–6 Ma ago, a general increase in African tectonic activity led to formation of the Western Rift (Ebinger 1989). A major episode of uplift coincided with the climatic changes ca. 2.5 Ma ago (Partridge and Maud 1987). After 6 Ma ago, the rift system continued to propagate to the southwest toward the Kalahari Craton (Summerfield 1996). One incipient zone of rifting, trending southwest from Lake Tanganyika, terminates in central Botswana, where faulting and tilting of the zonal margins have resulted in damming of the Okavango River to spread out as the extensive inland Okavango Delta (Scholz et al. 1976).

I suggest that the dynamics of the hydrological features associated with rifting – rivers redirected, lakes forming and disappearing, and especially the inland deltas spreading at the margins of incipient rift zones – have had a particular impact on the evolution of hominins and other biota. All early hominins required permanent water, and many of the eastern African hominin sequences reflect riverine and rift margin associated deltaic and lake environments (e.g., Harris et al. 1988; Brown and Feibel 1991). The significance of inland deltas is that they can form vicariated "islands" of mesic conditions – or refugia – throughout periods of aridification and even in the absence of topographic heterogeneity. The edges of such a refugium are ecologically heterogeneous with intrusions of the arid surrounding environment. ("Refugium" here means a biome refugium, e.g., a forest refugium preserves the characteristic forest vegetation physiognomy, although its detailed taxonomic composition may differ from that of the parent forest community.) The Okavango Delta provides a good example: it is a vicariant island – despite the very low relief of the area (Scholz et al. 1976) – of woodland savanna and water almost entirely surrounded by semidesert. Many of the hominin-bearing strata represent times when the areas were such inland deltaic-riverine-lacustrine refugia (Vrba 1988). This poses problems for our ability to recognize times of widespread climatic change across the larger areas because "climatic change in the larger region is recorded in a refugium only close to its ecotonal limits, by the new appearances (or disappearances) of peripheral taxa . . . that represent occasional intrusive elements from the alternative biome" (p. 410). An important implication from the evolutionary perspective is this: as climatic changes were sweeping across much of Africa at the Milankovitch scale, such inland deltas were recurrently isolated and reconnected as parts of larger continuous biomes. During the reconnected phases, migration and gene flow occurred. During the vicariant phases, there was enhanced incidence of gene pool divergence among populations, selection pressures at the refugial margins, intraspecific phenotypic diversification, and speciation. If it is true that inland deltas can in this way act as centers of phenotypic diversity and speciation and that they are particularly prevalent at the tilting margins of incipient rift zones, this would predict a late Neogene propagation of centers of increased speciation in a South-southwesterly direction as the rift evolved.

The Record of First Appearances of Mammalian Species

All Larger Mammals. As noted above, a method which corrects for the “gap bias” was applied to the African larger mammal record of the past 10 Ma. Such correction is especially important in the late Neogene climatic context because open, mesic to arid areas tend to preserve vertebrate fossils better than do the more forested, wetter ones (Hare 1980). The following results emerged (largely agreeing with those in Vrba 1995c, 2000, in so far as they are comparable): over the past 8 Ma, the strongest turnover pulses, involving both origination and extinction, occurred in the 5.5–5.0 Ma and 3.0–2.5 Ma intervals. (The dating of the earlier pulse is tentative as there are no physical dates, and this event may belong to the 6.0–5.5 Ma interval; I will refer to the 5.5 Ma event.) Each of the intervals 7–6.5 Ma and 3.5–3.0 Ma had an origination pulse without an extinction pulse and 1.0–0.5 Ma ago an extinction pulse without an origination pulse. Where one can compare this set of turnover events with the strongest cooling trends, the coincidence in time and intensity is strikingly close: the strongest climatic event, cooling toward ~2.5 Ma ago, coincides with the strongest turnover pulse, while lesser cooling and turnover events are present in the intervals 3.5–3.0 Ma and 1.0–0.5 Ma. The results also showed intervals of significantly low origination and extinction, some of which overlapped with periods of high sea level with low polar ice on a warmer earth (Haq et al. 1987; Hodell and Warnke 1991).

The African mammalian record and the bias-correction model which was used continue to be updated. The results do give preliminary support to the hypothesis that at least a substantial part of turnover in African mammals was initiated by climatic change and that global cooling with increased aridity and increased seasonality was a more important stimulus of turnover than was global warming (Vrba 2000, 2005). Of the cooling trends, the one toward 2.5 Ma was the strongest, followed by a lesser trend starting ca. 1 Ma ago. Yet individual glacial maxima became colder after 2.5 Ma, especially after 1 Ma (Shackleton 1995). The fact that there were no further major origination pulses after 2.5 Ma suggests that most of the lineages present then were either species that had evolved during the start of the modern ice age with adaptations to the new environments or long-lasting biome generalists that survived right through that cooling trend.

A related result is that of Vrba and DeGusta (2004). We studied the question of whether most species “start small,” namely, in geographic distributions that are more restricted than those they attain later on. We used the same 10 Ma-long record of the African larger mammals and the correction for the "gap bias." The number of fossil site records from which each species is known in an interval was taken as a proxy for the magnitude of its living geographic range and abundance in that interval. We then tested H_0 that the geographic spread of species remained averagely constant across successive survivorship categories, namely, from the first appearance (FAD) interval to the immediately following one, and so on. We found that the mean number of site records increased strongly from the FAD interval to the following survivorship interval, followed by a less marked although still significant increase to the next interval, with no significant changes thereafter. Thus we concluded that the average large African mammal species has indeed started its life in a relatively small population and thereafter increased in geographic range to reach its long-term equilibrium abundance by ca. 1 Ma after origin. This supports hypotheses of speciation that accord a major role to the formation of isolated populations of reduced size initiated by physical change.

Not everyone has agreed that global change was a driver of evolutionary change and speciation in African hominins and other mammals. For instance, one aim of Behrensmeyer et al. (1997) was to test Vrba's (1995c) finding of a turnover pulse in African mammals between ca. 2.8 and 2.5 Ma by examining the past 4.5 Ma in the Turkana Basin (including the northern Shungura Formation, Ethiopia, and the southwestern Nachukui and southeastern Koobi Fora Formations in Kenya). They concluded that there was "no major turnover event between 3.0 and 2.5 Ma" (p. 1591) and that this "weakens the case for rapid climatic forcing of continent-scale … faunal turnover" (p. 1593). I have reservations about their methods and assumptions which differed substantially from mine (Vrba 2005). A reexamination of Turkana Basin evolution over 4.0–1.0 Ma divided into 0.5 Ma-long intervals, using my African mammal database and the statistical "gap bias" model outlined above, showed a single significant origination pulse in the 3.0–2.5 Ma interval and no extinction pulses (Vrba 2005). Separate examination of the northern and two southern areas of the Turkana Basin indicated a strong speciation (and extinction) pulse in the North 3.0–2.5 Ma ago, but none in the combined or separate southern areas. This result is consistent with the southward spread of the Sahara Desert in the latest Pliocene (Dupont and Leroy 1995), which affected the northern basin more strongly, eliciting significant turnover, while the southern deltaic-lacustrine areas may have behaved more nearly like biome refugia. More recently, Bobé and Behrensmeyer (2004:399) found that between 4 and 1 Ma in the Turkana Basin, "episodes of relatively high faunal turnover occurred in the intervals 3.4–3.2, 2.8–2.6, 2.4–2.2, and 2.0–1.8 Ma. *Paranthropus* and *Homo* appear in the Turkana Basin during successive intervals of high turnover at 2.8–2.6 and at 2.4–2.2 Ma, while the appearance of *Homo erectus* is coupled to a major episode of turnover and grassland expansion after 2 Ma." (See also Bobé's 2011, comprehensive overview.)

At least some studies show that the larger mammalian turnover pattern is also reflected in small mammals. Among micromammals of the Shungura Formation, Ethiopia (Wesselman 1995), at 2.9 Ma woodland taxa predominated and even rainforest taxa were present (e.g., the bush baby *Galago demidovii*, a rainforest species today). These forms were displaced by new grassland-to-semidesert species by 2.4 Ma. The turnover includes terminal extinctions, immigrants from Eurasia such as a hare, *Lepus*, and global first appearances of species, such as a new species of *Heterocephalus*, the genus of desert-adapted naked mole rats, and a new species of the ground squirrel genus *Xerus* (Wesselman 1995). This time also marks the first African and global debuts in the record of several species of bipedal, steppe-, and desert-adapted rodents, such as the genus *Jaculus* of desert gerboas (Wesselman 1995) and a new springhare species, *Pedetes*, in South Africa.

Evidence for turnover pulses has by now been found in many records from different continents and time intervals and in diverse taxa, from marine invertebrates (e.g., Lieberman 1999) to mammals in areas beyond Africa (e.g., Azanza et al. 2000; Raia et al. 2005; van Dam et al. 2006). The last study, of a dense, long (24.5–2.5 Ma) record of rodent lineages from Spain, adds an intriguing element. It showed the existence of turnover cycles with periods of 2.4–2.5 and 1.0 Ma, which van Dam et al. (2006) linked to low-frequency modulations of Milankovitch oscillations. Specifically, the pulses of turnover occur at minima of the 2.37 Ma eccentricity cycle and nodes of the 1.2 Ma yr obliquity cycle. Obliquity nodes and eccentricity minima are associated with ice sheet expansion and cooling and affect regional precipitation. As the average duration of African larger mammal species over the past 20 Ma is close to the period of the eccentricity cycle (2.33 Ma, Vrba and DeGusta 2004), the question arises: did a substantial proportion of those species originate at one eccentricity minimum, and become extinct at the next, and could hominins have been a part of that?

The Hominin Record. The hominid sample is too small (15 to more than 20 species depending on which sources are consulted) to test whether most hominin species "started small" and to test for turnover pulses using the statistical methods which were applied to all larger mammals. Nevertheless it is of interest to compare the known hominin FAD record with the timing of major climatic trends and speciation pulses in all larger African mammals. The earliest appearance of hominins, *Sahelanthropus* from Chad (Brunet et al. 2004), is ca. 7.2–6.8 Ma according to Lebatard et al. (2008). The hominin clade originated 8–5 Ma ago based on molecular estimates (Ruvolo 1997). Thus, the first appearance of hominins in the record participates in the elevated mammalian origination toward 6.5 Ma ago, in an interval marked by increased African tectonic activity (Ebinger 1989), and ice buildup in West Antarctica with global cooling (Kennett 1995). The FAD of *Orrorin tugenensis* ca. 6 Ma (Senut et al. 2001; Sawada et al. 2002) occurs near the end of the strong and widespread decrease in tree cover and increased aridity over ca. 6.3 and 6 Ma reported by Bonnefille's (2010). The genus *Ardipithecus* from the Middle Awash area, Ethiopia, includes two species to date: *A. kadabba* from the western margin in 5.7–5.2 Ma-old strata (Haile-Selassie 2001; Haile-Selassie et al. 2009) and *A. ramidus* dated 4.4–4.2 Ma at Aramis (White et al. 1994; WoldeGabriel et al. 1994; White, Asfaw et al. 2009) and with a similar date at Gona Western Margin (bracketed 4.51–4.32 Ma, Semaw et al. 2005). Thus, the FAD of *Ardipithecus* is associated temporally (and possibly also causally) with the major climatic changes which accompanied the Messinian ca. 5.8–5.3 Ma ago and with the ca. 5.5 Ma turnover event in African mammals.

Most African FADs of hominin species are mid-Pliocene to mid-Pleistocene in age, during which time the intervals of strongest climatic change were (see review above) 4.2–3.9 Ma, 3.5–3.2 Ma, 2.9–2.3 Ma, 1.8–1.6 Ma, 1.2 Ma, and 1.0–0.6 Ma and possibly also near 2 Ma and 4 Ma. Together, these episodes occupy ca. 40 % of the past 5 Ma. Yet most, and possibly all, of the hominin FADs either coincide with or fall very close to one of these events (chronology mostly after Wood and Richmond 2000; Wood and Leakey 2011): *Australopithecus anamensis* first appears at ca. 4.2 Ma and *A. afarensis* ca. 4.0 Ma (3.8 Ma or possibly 4 Ma according to Wood and Leakey 2011); FADs of *A. bahrelghazali*, *Kenyanthropus platyops* and possibly also *A. africanus* are a part of the mammalian origination pulse in the 3.5–3.0 Ma interval which may be a response to the cooling trend ca. 3.5–3.2 Ma; *Australopithecus garhi*, *Paranthropus aethiopicus*, *P. boisei*, and possibly also *Homo habilis* and *H. rudolfensis* have FADs in the 2.8–2.3 Ma interval. The FADs of *Australopithecus sediba* (Berger et al. 2010; Pickering et al. 2011), *H. ergaster*, and *H. erectus* (and its migration to Eurasia) between 2.0 and 1.8 Ma may also be associated with major climatic change. While taphonomic factors and chance may have contributed to this pattern, it does leave intact the hypothesis of climatic cause of at least most hominin speciation. An important splitting event in the hominin clade was the one that led to *Paranthropus* on the one hand and *Homo* on the other. Several systematic studies have concluded that the characters of *A. afarensis* are consistent with it being the common ancestor of *Paranthropus* and *Homo* and possibly also of one or more additional lineages (e.g., Kimbel 1995; Asfaw et al. 1999). After enduring in apparent equilibrium since ca. 4 Ma, *A. afarensis* is last recorded just after 3.0 Ma (Kimbel et al. 1994), while its descendants appear variously between 2.7 Ma and 2.3 Ma. Kimbel (1995:435) concluded: “regardless of which phylogenetic hypothesis is more accurate, it is clear that a pulse of speciation occurred in the hominin lineage between 3.0 and ca. 2.7 Ma, producing at least three lineages.” The phylogenetic pattern, of an inferred ancestor ending after 2.9, with new descendants branching off between 2.9 and 2.3 Ma ago, is common in bovids (e.g., Vrba 1995c, 1998a). These concordant genealogical patterns among different mammalian groups strongly suggest the causal influence of the start of the modern ice age, namely, that common causal rules connect the climate system with evolution of different biotic groups. It remains to be seen whether additional information in the future will support these preliminary indications that major changes in the mode of the climatic pattern and the concomitant changes in African environments were important causal influences on speciation in hominins, just as they were in many other mammalian lineages.

Climate in Relation to Habitats and Adaptations of Hominins

Bonnefille’s (2010) review of African vegetational evolution provides a particularly good context for this section because of its broad temporal and geographic scope, which encompasses the Cenozoic with focus on the past 10 Ma, includes the recent vegetation, and ranges right across the African tropics with emphasis on areas and sites which have yielded hominins. She discussed both the macrobotanical and the microbotanical evidence and its relationship to results from recent isotopic studies and from Atlantic and Indian Ocean deep-sea cores. Her conclusions include the following (Bonnefille 2010:409):

> the palaeontological hominid record so far documented appears embedded within a long evolution of tropical vegetation bracketed between two main events. These two events are the most pronounced among all of the many that occurred during the last 10 Ma. They had the strongest impact on past vegetation, at the continental scale, both in west central and eastern Africa..... The first event was a strong shift from an important forest expansion (7.5–7 Ma) to an abrupt retreat with minimum tree proportion (6.5–6 Ma) concerning the whole tropical region, half a million years before the Messinian salinity crisis. . . . The second event (2.7–2.5 Ma) was the arid shift, from forest to savanna expansion, corresponding to maximum expansion of the northern hemisphere glaciation. . . . [It involved] greater and more widespread aridity, increase in C_4 grass abundance in lowlands savanna and steppe, and the relative expansions of mountain forests coincide with the appearance of the genus *Homo* and stone tools registered simultaneously at different sites in East Africa.

Her summation stresses how pervasive mixed vegetation types are in tropical Africa, namely, areas which include both wooded and open habitat in close geographic proximity (p. 409): “*Mixed tree and grass cover* are among the widely spread vegetation conditions [and have] *persisted throughout the last 10 Ma*.”

I have added the italic emphasis in the last sentence because it reflects a convergent theme in early hominin environmental research over the past decade, as apparent in the following discussion of the hominin species in terms of their natural surroundings, adaptations, and habits: the vegetational and other local conditions surrounding each of the early hominin species were heterogeneous and mosaic.

The earliest known hominins (or presumed members of the hominin clade; not all agree) are *Sahelanthropus tchadensis* (Brunet et al. 2002), ca. 7 Ma old, and *Orrorin tugenensis* (Senut et al. 2001) from Lukeino, Kenya, ca. 6–5.7 Ma (Sawada et al. 2002). The associated fauna of *Sahelanthropus* according to Brunet et al. (2005:753) “indicates a mosaic of landscapes probably resembling that of the present-day Okavango Delta (Botswana).” The Okavango Delta today “is an interlocking mosaic of habitat types” (Paterson 1976:55). These range from permanent swamp, wetlands, and seasonally inundated open areas, through higher-lying grasslands, dry scrub, woodland, to very dense woodland with high and nearly closed tree canopy and water margin forest, and many of the mammal species are virtually confined to particular parts of this mosaic (Ramberg et al. 2006).

The environment of *Orrorin* was initially described as follows by Senut (2006:89): “It has been widely accepted that hominins (and thus bipedalism) emerged in a savannah environment. However, it is now clear that the earliest bipeds are associated with forested environments as proved by the flora and the fauna of the Lukeino Formation (Kenya, 6 Ma).” But detailed studies of the mammals indicated a more heterogeneous environment (Mein and Pickford’s 2006:183 micromammal study):

> The presence of galagids, fruit bats and the diversity of dendromurines (3 species) and some probably arboreal murids (possibly ancestral to *Thallomys* or *Grammomys*) indicates the presence of trees in the vicinity of the site, but some of the taxa suggest the presence of

> relatively open environments in the vicinity of Kapsomin at the time of deposition. A similar mixture of vegetation types is indicated by the large mammals from Lukeino.

Bonnefille (2010) linked the strong decrease in tree cover in both East and West Africa after 7 Ma to the earliest hominins as follows (p. 390):

> At that time, very arid conditions shown by scarce tree cover occurred over the whole tropical region. … Generally arid conditions coincide with the accepted timing for the chimpanzee/hominid split, and record of *Sahelanthropus tchadensis* in Chad and *Orrorin tugenensis* in Kenya, although these fossils were found under locally wooded environment.

This underlines the important point that patterns and causal actions at different hierarchical levels should not be conflated, because they are to some extent decoupled and relate only indirectly and in subtle ways: at the more inclusive climatic level "very arid conditions" and "scarce tree cover [spread] over the whole tropical region," just as at the higher phylogenetic level of species, there were changes in population structure toward vicariance that in some cases resulted in speciation and extinction. At the more local scale were those "habitat islands," each with its "interlocking mosaic of habitat types," in Paterson's (1976) words, and buffered to some extent from the larger geographic pattern of aridity and low wood cover, with the hominins and other organisms adapting to those local conditions. We still know very little about what the earliest hominids were doing. Bipedal locomotion of some kind has been claimed for both *Sahelanthropus* (Brunet et al. 2002) and *Orrorin* (Pickford et al. 2002), although doubts on that have been expressed, for example, by Harcourt-Smith and Aiello (2004), who considered that the earliest evidence for bipedalism is only arguably from *Sahelanthropus*, *Orrorin*, and the next taxon discussed here, *Ardipithecus*.

Ever since the announcement of *Ardipithecus ramidus* as a candidate for the "long-sought potential root species for the Hominidae" (White et al. 1994:306, who described it as *Australopithecus ramidus*), there has been a debate about its morphology, phylogenetic position, and its habitat 4.4 Ma ago at the source site Aramis. Some of the unexpected and astonishing features and implications of this taxon, especially after subsequent discovery that more than 110 additional specimens from 4.4 Ma stratum include a partial skeleton with much of the skull, hands, feet, limbs, and pelvis, are reflected by the following statements by White, Asfaw et al. (2009:75):

> This hominid combined arboreal palmigrade clambering and careful climbing with a form of terrestrial bipedality more primitive than that of *Australopithecus*. *Ar. ramidus* had a reduced canine/premolar complex and a little-derived cranial morphology and consumed a predominantly C_3 plant-based diet (plants using the C_3 photosynthetic pathway). Its ecological habitat appears to have been largely woodland-focused. *Ar. ramidus* lacks any characters typical of suspension, vertical climbing, or knuckle-walking. *Ar. ramidus* indicates that despite the genetic similarities of living humans and chimpanzees, the ancestor we last shared probably differed substantially from any extant African ape. Hominins and extant African apes have each become highly specialized through very different evolutionary pathways.

Concerning the Aramis habitat, White, Ambrose et al. (2009) wrote (p. 87):

> Assessment of dental mesowear, microwear, and stable isotopes from these and a wider range of abundant associated larger mammals indicates that the local habitat at Aramis was

> predominantly woodland. The *Ar. ramidus* enamel isotope values indicate a minimal C_4 vegetation component in its diet (plants using the C_4 photosynthetic pathway), which is consistent with predominantly forest/woodland feeding. Although the Early Pliocene Afar included a range of environments, and the local environment at Aramis and its vicinity ranged from forests to wooded grasslands, the integration of available physical and biological evidence establishes *Ar. ramidus* as a denizen of the closed habitats along this continuum.

In their response to White, Ambrose et al. (2009) and also to companion papers by WoldeGabriel et al. (2009) and Louchart et al. (2009), Cerling et al. (2010) disagreed and stated that from their analysis of the stable isotopic record (p. 1105d): "we find the environmental context of *Ar. ramidus* at Aramis to be represented by what is commonly referred to as tree-or bush-savanna, with 25 % or less woody canopy cover," and that "although we do not judge the validity of the savanna hypothesis, we note that from the stable isotopic record, the connection between bipedalism and C_4 grass expansion starting in the late Miocene and continuing into the Pliocene remains a viable idea." White et al. (2010) replied that Cerling et al.'s (2010) reconstruction of a predominantly open grassland environment with riparian woodland is inconsistent with a wealth of fossil, geological, and geochemical evidence. While they acknowledged that the local environment in the vicinity of Aramis ranged from dense woodland/forest to wooded grassland, White et al. (2010:1105) held firm that "in the Middle Awash, *Ar. ramidus* fossils are confined to the western portion of the sampled Pliocene landscape where the species is associated with woodland to grassy woodland habitat indicators." More recently, Cerling et al. (2011) investigated the percentages of woody cover, using stable carbon isotopes, in fossil soils from hominin sites in the Awash and Omo-Turkana basins. They concluded (p. 55) that "the combined results from two of the most significant hominid-bearing regions in eastern Africa leave the savanna hypothesis as a viable scenario for explaining the context of earliest bipedalism, as well as potentially later evolutionary innovations within the hominin clade."

As coauthors of White, Ambrose et al. (2009), David DeGusta and I contributed inference of the paleohabitat based on bovid astragali (DeGusta and Vrba 2003), especially of the overwhelmingly most common species which is a tragelaphine antelope, namely, that 4 Ma ago in Aramis, *A. ramidus* lived in (or at least spent a lot of time in) a woodland habitat. Additional inferences from the bovids suggest that there were wetlands and water bodies nearby (thus, Louchart et al.'s 2009:66e1, conclusion that the woodlands were "distant from large water bodies" is not one I share) and that there were also grassland areas in the vicinity. Namely, the notion that the Aramis environment was a mosaic of habitats among which *A. ramidus* preferred the dense woodlands seemed (and still seems) reasonable to me. I wonder whether we may find future support for the hypothesis that, since ape ancestry, *Ardipithecus* had already diverged toward a measure of broader use of environmental resources and the more generalized ability to live within a vegetationally mosaic environment. The results of Levin et al. (2008) give encouragement to consider this possibility seriously. They concluded (Levin et al. 2008:215) that

> the spectra of isotopic results from herbivores found in late Miocene *Ar. kadabba* and early Pliocene *Ar. ramidus* sites at Gona are most similar to isotopic values from extant herbivores living in bushland and grassland regions and dissimilar to those from herbivores living in closed-canopy forests, montane forests, and high-elevation grasslands. The tooth enamel isotopic data from fossil herbivores make it clear that *Ardipithecus* at Gona lived among a guild of animals whose diet was dominated by C_4 grass, and where there is no record of closed-canopy vegetation.

However, the notion that *A. ramidus* at Aramis was tied to – or at least strongly preferred – woodlands (albeit situated in a mosaic of habitats) seems to be compatible with what Semaw et al. (2005:301) reported for *Ardipithecus ramidus* from As Duma, Gona, Ethiopia, that "the Early Pliocene As Duma sediments sample a moderate rainfall woodland and woodland/grassland."

Kimbel et al. (2006) argued persuasively that *A. anamensis* and *A. afarensis* represent parts of an anagenetically evolving lineage or evolutionary species. In Bonnefille's (2010) broad overview of the large-scale African changes which led to the origin and establishment of this lineage, she noted that the period from 6 to 4 Ma was marked by a progressive increase in tree cover that culminated at 3.9 Ma, during *A. anamensis* time and before the first appearance of *A. afarensis*. From their stable isotope-based diet reconstructions of Turkana Basin hominins, Cerling et al. (2013:10501) concluded that "*Australopithecus anamensis* derived nearly all of its diet from C_3 resources . . . [while] by ca. 3.3 Ma, the later *Kenyanthropus platyops* had a very wide dietary range-from virtually a purely C_3 resource-based diet to one dominated by C_4 resources."

Bedaso et al. (2013) used carbon and oxygen isotopes of mammalian tooth enamel to reconstruct paleoenvironments of *A. afarensis* from the Basal Member (ca. 3.8–3.42 Ma) and the Sidi Hakoma Member (3.42–3.24 Ma) of the Hadar Formation in the Middle Pliocene locality of Dikika, Ethiopia. Their results indicate a wide range of foraging strategies, characterized by mixed C_3/C_4 to C_4-dominated diets in wooded grasslands to open woodlands and that (2013)

> the middle Pliocene habitat structure at Dikika could be as diverse as open grassland and wooded grassland, and woodland to forest in the Sidi Hakoma Member while wooded grassland, woodland to grassland are evident in the Basal Member. All habitats except closed woodland and forest are persistent through both members; however, the relative proportion of individual habitats changed through time. . . . Thus, the existence of *A. afarensis* throughout the middle Pliocene indicates either this species might have adapted to a wide range of habitats, or its preferred habitat was not affected by the observed environmental changes.

Kingston and Harrison (2006) used similar methods and reached similar conclusions on a heterogeneous environment for *A. afarensis* from the Laetoli Beds in Tanzania, much further south. While over the long term many African records show that cooling was accompanied by aridification, it is by no means an invariable association, as expected from the shifting phase relationship between the monsoon and glacial cycles. For example, pollen data from Hadar, Ethiopia, show that "*Australopithecus afarensis* accommodated to substantial environmental variability between 3.4 and 2.9 Ma ago. A large biome shift, up to 5 °C cooling, and a 200- to

300-mm/year rainfall increase occurred just before 3.3 Ma ago, which is consistent with a global marine delta^{18}O isotopic shift" (Bonnefille et al. 2004:12125).

Wood and Richmond (2000) considered the tibia of *Australopithecus anamensis* (ca. 4.2 Ma; Leakey et al. 1995) the earliest undisputed evidence of bipedalism and in thinking about the ecology of the *anamensis-afarensis* lineage, recall the debate on selective factors which might have promoted the inception and advancement of bipedalism. Much new evidence now clearly indicates that the relevant lineages since the late Miocene were probably all living in patchy environments, mosaics of habitat types, with patches of dense woodland and forest, light woodland, grassland, and interrupted by barriers such as volcanic deposits and watered areas including seasonally flooded wetlands. Selection pressure for traversing the barriers to reach resources on the other side (which may have been what the *A. afarensis* individuals who formed the Laetoli footprints were doing; Leakey and Hay 1979), or for foraging in these areas (as in a shallow delta or wetland) might have promoted the onset or, later on, elaboration of bipedality. The notion that wading in shallow water played a part (Niemitz 2000; Verhaegen et al. 2002) seems reasonable given what we know about the palaeoenvironments of many early hominid species. In such a mosaic context some additional previous hypotheses of what caused the adoption of upright posture may apply: carrying, display or warning, new feeding adaptations, control of body temperature, tools, and stone throwing. Reviews are given by McHenry (1982), who thought that hominin bipedalism "could have arisen as an energetically efficient mode of terrestrial locomotion for a small_bodied hominoid moving between arboreal feeding sites" (p. 163), and by Preuschoft (2004).

Whatever the combination of selective forces, there is much healthy debate on how the postcranial anatomy of early hominins should be interpreted in terms of function, habitat use, and phylogenetic relationships. Harcourt-Smith and Aiello (2004)) reviewed some of the evidence (including the Laetoli footprints, the AL 288-1 *A. afarensis* skeleton, postcranial material from Koobi Fora, the Nariokotome *H. ergaster* skeleton, "Little Foot" [StW 573] from Sterkfontein, South Africa, fossils of *Orrorin*, *Ardipithecus*, and *Sahelanthropus*) and pointed out the greater diversity in bipedalism (or putative bipedalism) in earlier hominins than previously suspected. In each of their three phylogenetic scenarios (Harcourt-Smith and Aiello 2004: Fig. 4), the postcranial diversification coincides broadly with the 3.0–2.3 Ma period of the largest Pliocene climatic trend. More recently, Haile-Selassie et al. (2012) reported a new hominin foot from a new site Woranso-Mille in the central Afar, Ethiopia, which further increases the diversity of Pliocene bipedal adaptations. They wrote (p. 565):

> Here we show that new pedal elements, dated to about 3.4 Ma ago, belong to a species that does not match the contemporaneous *Australopithecus afarensis* in its morphology and inferred locomotor adaptations, but instead are more similar to the earlier *Ardipithecus ramidus* in possessing an opposable great toe. This not only indicates the presence of more than one hominin species at the beginning of the Late Pliocene of eastern Africa, but also indicates the persistence of a species with *Ar. ramidus*-like locomotor adaptation into the Late Pliocene.

There has also been input from South Africa into the debate on diversity and environmental associations of hominin locomotion. Clarke and Tobias (1995) proposed that the foot bones from Sterkfontein Member 2 (StW 573, Little Foot, dated ca. 4 Ma, Partridge et al. 2003, see below) reflect a foot that had not sacrificed arboreal competence or hallucial opposability and that this suggests dense tree cover in the environment. Based on fossil pollen, it has been suggested that the preferred habitat of *A. africanus* at Makapansgat was subtropical forest and that selective pressures associated with densely vegetated environments played a role in the evolution of bipedalism (Cadman and Rayner 1989; Rayner et al. 1993). Potts (1998a) dubbed this the "forest hypothesis" of bipedal origin. The fossil bovids associated with *A. africanus* at Makapansgat and Sterkfontein do not suggest a uniform forest, although a mosaic in the greater area which includes dense and open woodland patches, as well as grassy patches and permanent water, could be consistent (Vrba 1974, 1980, 1987b), which agrees with Reed's (1997) conclusions. A related insight comes from Lee-Thorp et al.'s (2010) analysis of stable isotopes in the tooth enamel of more than 40 hominin specimens, including *A. africanus* from Makapansgat and Sterkfontein and *Paranthropus robustus* from Swartkrans and Kromdraai together spanning ca. 3–1.5 Ma. They concluded (p. 3389) that among all these South African australopithecines including *A. africanus* and persisting over the entire time range, "these data demonstrate significant contributions to the diet of carbon originally fixed by C_4 photosynthesis, consisting of C_4 tropical/savannah grasses and certain sedges, and/or animals eating C_4 foods. Moreover, high-resolution analysis of tooth enamel reveals strong intra-tooth variability in many cases, suggesting seasonal-scale dietary shifts." (See also Sponheimer et al. 2013.) These results suggest spatial variability in vegetation cover and also seasonal variability, rather than predominant forest.

Australopithecus afarensis, which persisted in place through major climatic and vegetational variability (e.g., at Hadar, Bonnefille et al. 2004; Bedaso et al. 2013), appears to have been the most generalist of all hominin species up to the Middle Pliocene. It was geographically so widespread that in the past one wondered why it was not also found among the South African hominins. The findings of Partridge et al. (2003) suggested that the *anamensis-afarensis* lineage may well have been present there as well: based on cosmogenic aluminum-26 and beryllium-10 burial dates of low-lying fossiliferous breccia in the Sterkfontein caves, associated hominin fossils such as skeleton StW 573 date to ca. 4 Ma, the time of the *anamensis-afarensis* transition in East Africa.

An important splitting event in the hominin clade was the one that led to *Paranthropus* on the one hand and *Homo* on the other. Several systematic studies have concluded that the characters of *A. afarensis* are consistent with it being the common ancestor of *Paranthropus* and *Homo* and possibly also of one or more additional lineages (e.g., Kimbel 1995; Asfaw et al. 1999). After enduring in apparent equilibrium since ca. 4 Ma, *A. afarensis* is last recorded just after 3.0 Ma (Kimbel et al. 1994), while its descendants appear variously between 2.7 Ma and 2.3 Ma. Kimbel (1995:435) concluded that "regardless of which phylogenetic hypothesis is more accurate, it is clear that a pulse of speciation occurred in the hominin lineage between 3.0 and ca. 2.7 Ma, producing at least three lineages." The phylogenetic pattern, of an inferred ancestor ending after 3.0 Ma, with new descendants branching off between that and 2.3 Ma ago, is common in bovids (e.g., Vrba 1995c, 1998a).

According to Wood (1995), the first signs of the "hypermasticatory trend" occurred with an advent of *Paranthropus aethiopicus* ca. 2.6 Ma ago, followed by exaggeration in this trend ca. 2.3 Ma with the FAD of *P. boisei*, and further lesser modifications to the dentition of this species between 1.9 and 1.7 Ma. Efforts to find out what the robust australopithecines were eating, and where they lived, have been ongoing for a long time. A study which uses functional morphology of mammalian assemblages associated with early hominins to reconstruct their environs by Reed (1997) is particularly useful because it treats the East and South African Plio-Pleistocene fossil assemblages in the same analysis, comparing them with each other and with extant mammalian communities from different habitat types. Reed (1997) concluded that *Paranthropus* species in East and South Africa lived in both wooded and more open environments, always in habitats that include wetlands. This is compatible with our earlier findings for the relevant South African sites, based on bovid abundances (Vrba 1975) and also on the assemblages as a whole (Brain 1981b), which indicated environs of *P. robustus* including substantial grassland with wooded patches and permanent water indicated by water-dependent fauna.

The notion that robust australopithecines, *Paranthropus*, were in certain senses specialists was originally proposed by Robinson (1963) based on the dentition of *P. robustus*. He suggested that the "crushing, grinding" robust vegetarian specialist lived in a somewhat wetter and more luxuriant environment than did the earlier gracile omnivore *A. africanus*. Prompted by the bovid evidence of change to more open vegetation in the *Paranthropus*- and *Homo*-bearing strata, compared to the earlier South African ones with only *A. africanus*, the question arose whether the musculature of *P. robustus* was massive and the molars proportionally so large "because their 'vegetables' were of the tough grassland type" (Vrba 1975:302) and whether, in contrast to the more generalized *Homo*, robust australopithecines may have been more specialized on open and relatively more arid habitats. Based on comparisons of the dental microwear of *A. africanus* and *P. robustus*, Grine (1981, 1986) concluded that the latter had probably processed tougher food items. Wood and Strait (2003) did a thorough analysis of the proposal that *Paranthropus* species were feeding specialists. They concluded that *Paranthropus* species were most likely ecological generalists (i.e., eurybiomic in being able to make a living in varied environments) and made the novel proposal that (p. 149) ". . . although the masticatory features of *Paranthropus* are most likely adaptations for consuming hard or gritty foods, they had the effect of broadening, not narrowing, the range of food items consumed." I accepted their arguments because the acquisition, in response to newly encountered environments, of morphology which can perform a new specialized function but which at the same time permits the retention of functions evolved in the ancestral more uniform environment, is a recurrent theme in the evolution of generalist mammals (e.g., the impala *Aepyceros melampus* which, from a browsing ancestry, Vrba and Schaller 2000, evolved cranial and dental features which allow mastication of grass and other tough plant matter and also a stomach structure which undergoes reversible seasonal changes, Hofmann 1973, a rare adaptation to varied vegetational environments. As a consequence of these dental and digestive evolutionary advances, the impala is today a consummate herbivore generalist which can subsist in different environments by switching its dietary intake).

A number of isotopic analyses of diet and environment have since contributed to illuminating such questions. van der Merwe et al. (2008) did isotopic dietary studies of *H. habilis* and *P. boisei* teeth from Olduvai, Tanzania, and discussed how the results compare with previous ones for the South African hominins (see citation of Lee-Thorp et al. 2010, above). They found that the two Olduvai species had very different diets, while, in contrast, the isotopic analyses of the three South African species of early hominins, *A. africanus*, *P. robustus*, and *Homo* sp., showed considerable variation in individual diets but no marked differences between species. For two Olduvai specimens of *P. boisei*, van der Merwe et al. (2008) found C_4 dietary components (77 % and 81 %) that far exceeded those of the South African taxa, including *P. robustus*, and indeed of all other early hominins for which carbon isotope values were available by that time. They pointed out that the C_4 input could come from consuming grasses, some sedges and forbs, and a variety of animals which eat C_4 plants and suggested that *P. boisei* may have fed on papyrus or other C_4 species of Cyperaceae which are perennially available near water. A similar study by Cerling et al. (2013) on hominins in the Turkana Basin showed comparable results: by ca. 2 Ma, specimens attributable to the genus *Homo* provide evidence for a diet with a ca. 65/35 ratio of C_3- to C_4-based resources, whereas *P. boisei* had a higher fraction of C_4-based diet (ca. 25/75 ratio). Thereafter *Homo* sp. increased the fraction of C_4-based resources in the diet through ca. 1.5 Ma, whereas *P. boisei* maintained its high dependency on C_4-derived resources. Sponheimer et al. (2013:10513) summarized their overview of isotopic evidence of early hominin diet as follows:

> Before 4 Ma, hominins had diets that were dominated by C_3 resources and were, in that sense, similar to extant chimpanzees. By about 3.5 Ma, multiple hominin taxa began incorporating ^{13}C-enriched [C_4 or crassulacean acid metabolism (CAM)] foods in their diets and had highly variable carbon isotope compositions which are atypical for African mammals. By about 2.5 Ma, *Paranthropus* in eastern Africa diverged toward C_4/CAM specialization and occupied an isotopic niche unknown in catarrhine primates, except in the fossil relations of grass-eating geladas (*Theropithecus gelada*). At the same time, other taxa (e. g., *Australopithecus africanus*) continued to have highly mixed and varied C_4 diets.

Together all the available lines of evidence for species of *Paranthropus* support a degree of generalism in terms of the patchiness, from open to more wooded, of vegetational environments they inhabited and dietary specialization in the east African species yet not in the southern *P. robustus* which evidently maintained a more mixed diet in terms of the range of C_3- to C_4-based resources. All these leave intact the possibility raised by Wood and Strait (2003) that the evolution of the masticatory features of *Paranthropus*, while allowing consumption of hard or gritty foods, may have broadened their options in the soft-to-hard-and-gritty spectrum of foods, perhaps remaining within the C_4/CAM range of plants in the case of *P. boisei* while ranging across both C_3 and C_4 resources in the case of the southern *P. robustus*.

There are two species with first appearances after the last record of *A. afarensis* which have been assigned to *Australopithecus*. The specific name *Australopithecus garhi* reflects well the reactions of many ("garhi" means "surprise" in the Afar language) when they found out about the mosaic combination of its anatomical features relative to previously known hominins and the tantalizing associated evidence of cultural advances (which may or may not be the handiwork of this species), all at the hitherto under-represented age of 2.5 Ma (Asfaw et al. 1999; de Heinzelin et al. 1999). The cranial and dental remains, from the Hata beds, Bouri Formation, of Ethiopia's Middle Awash, led Asfaw et al. to conclude that (p. 629) *A. garhi* "is descended from *Australopithecus afarensis* and is a candidate ancestor for early *Homo*. Contemporary postcranial remains feature a derived humanlike humeral/femoral ratio and an apelike upper arm-to-lower arm ratio." The abundant vertebrate remains together with the sedimentology indicate an environment (de Heinzelin et al. 1999:626) that was "primarily lake marginal. Alcelaphine bovids are abundant and diverse. All indicators point to a broad featureless margin of a freshwater lake. Minor changes in lake level, which were brought about by fluctuating water input, would probably have maintained broad grassy plains leading to the water's edge." With *A. garhi* are found some of the earliest made stone tools with earliest evidence of the their use to butcher large mammals (p. 625):

> Spatially associated zooarchaeological remains show that hominins acquired meat and marrow by 2.5 Ma ago and that they are the near contemporary of Oldowan artifacts at nearby Gona. The combined evidence suggests that behavioral changes associated with Lithic technology and enhanced carnivory may have been coincident with the emergence of the *Homo* clade from *Australopithecus afarensis* in eastern Africa.

One of the specimens on which unambiguous cutmarks are visible, perhaps made during tongue removal, was identifiable to a new genus and species of a medium-sized bovid (of body size comparable to living hartebeests) in the tribe Alcelaphini, a tribe and bovid size class which are very abundant not only in this Hata Member but also were appearing in greater numbers than before all over Africa near 2.5 Ma. Looking at this earliest evidence of cutmarks made by hominins, in its faunal and environmental context, prompts one to think about the arguments of Owen-Smith (2013) who contrasted the Pleistocene large herbivore faunas of the southern continents and argued (p. 1215) that it was the African "abundance and diversity of medium-sized grazing ruminants unrivalled elsewhere ... that facilitated the adaptive transition by early hominins from plant-gatherers to meat-scavengers."

Only a few years ago, another new species of hominin was announced, *Australopithecus sediba*, based on two partial skeletons dated 2.0 Ma (by uranium-lead dating combined with paleomagnetic and stratigraphic analysis) from cave deposits at the Malapa site in South Africa (Berger et al. 2010; Dirks et al. 2010; Pickering et al. 2011). Berger et al. (2010:195) argue that *A. sediba* "is probably descended from *Australopithecus africanus*. Combined craniodental and postcranial evidence demonstrates that this new species shares more derived features with early *Homo* than any other australopith species and thus might help reveal the ancestor of that genus." The faunal fossils associated with *A. sediba* are as yet few, but consistent in chronological and environmental implications with what was found at the other hominin-associated sites thought to date near 2 Ma in the Sterkfontein area.

Near the end of the large late Pliocene cooling trend, by ca. 2.6–2.5 Ma, stone tools appeared in several other places (e.g., Semaw et al. 1997) besides the finds from Bouri, together with evidence of butchery already mentioned (de Heinzelin et al. 1999). Hatley and Kappelman (1980) proposed that the climatic change led to this behavioral advance. They showed that a high belowground plant biomass is characteristic of xeric open areas and argued that digging out of such foods, first by hand and later by digging sticks and other tools, evolved as an important feeding strategy of early hominins when the African savanna became more open and arid. Leakey (1971) noted early on that the onset of more expanded tool kits appears to overlap with the climatic change ca. 1.8–1.6 Ma ago. Another milestone dating to this time was proposed by Wood and Richmond (2000): the fact that the mandible and postcanine tooth crowns of *H. ergaster* (dated ca. 1.9–1.5 Ma) when scaled to body mass are no larger than those of modern humans may reflect the earliest cooking.

The late Pliocene and Pleistocene behavioral and cultural advances presumably reflect reorganization and expansion of the brain. The available evidence indicates significant increase in EQ (encephalization quotient) in *Homo* only over the past 2 Ma, with the largest EQ increase occurring ca. 600–150 Ka ago, according to Holloway (1970, 1972, 1978) and McHenry (1982). Shultz et al. (2012) found punctuated changes in encephalization at approximately 1.8 Ma, 1 Ma, and 100 Ka, noting that brain size change at ca. 100 Ka is coincident with demographic change and the appearance of fully modern language. Holloway et al. (2003) presented evidence that brain reorganization predated brain expansion in hominin evolution. I previously suggested that the encephalization trend in *Homo* "evolved by progressive prolongation of ancestral, fast, early brain growth phases. It started with the modern ice age, and was fuelled by progressive intensification of cooling minima since then" (Vrba 1996:15). I suspect that we may find future indications that some of the brain modifications which came to characterize *Homo* – perhaps not increase in EQ but brain reorganization – were promoted by the start of the modern ice age, which would be consistent with the proliferation of stone tool finds in the record by 2.6–2.5 Ma.

If the largest EQ increase did occur ca. 600–150 Ka ago (as cited above), it could be related to the end of the mid-Pleistocene strong climatic events ca. 1.0–0.6 Ma ago. Many selective scenarios for encephalization in *Homo* have been proposed. Falk's (1980) review included warfare, language, tools and labor, hunting, and heat stress. Gabow (1977) emphasized population structure and culture, McHenry (1982) language, and Brain (2001) our predatory past. Vrba (1985a, 1988, 1989a) proposed that major selection pressures that led to brain and cultural evolution derived from the large-scale changes in climatic mean and amplitude during the Plio-Pleistocene and that culture and the underlying brain modifications in *Homo* represent adaptation to eurybiomy or "generalist adaptation. Hominine culture is an extension of the common phenomenon in other animals that use behaviour to cope with climatic conditions . . . a special case among animal behaviors that confers an expanded use of environmental resources" (Vrba 1989a:30). As cited above, Potts (1998a) made a similar proposal to explain the brain and behavioral adaptations of *Homo*. Others have also argued that *Homo* evolved toward biome generalization (e.g., Wood and Strait 2003).

Morphological evidence of a commitment to long-range bipedalism (e.g., long legs, large femoral head) appeared much later, ca. 1.6 Ma, in the postcranial skeleton KNM-WT 15000 from Nariokotome, West Turkana (Brown et al. 1985, who assigned it to *H. erectus*; Wood and Richmond 2000 included it in *H. ergaster*). There is some agreement that the onset of advanced bipedalism in *Homo* ca. 1.6 Ma ago not only falls during a time of change to more open and seasonally arid landscapes (and near the advent of other novelties in hominin evolution, as noted above) but also makes sense as a selective response to these changes. Potts (1998a) pointed out that the latest Pliocene populations of *Homo* were increasingly mobile, for example, tool-making behavior involved long-distance transport of stones as far as 10 km. Increased mobility is reflected by the migration out of Africa by 1.8 Ma of a lineage of *Homo* (if the early date for *H. erectus* in Java, Indonesia, is correct, Swisher et al. 1994), the first of many subsequent migrations out of Africa which were associated with physical changes (Stringer 1995; Tattersall 1997b; Klein and Edgar 2002; see also Abbate and Sagri 2012, who found that the early to Middle Pleistocene *Homo* dispersals from Africa to Eurasia were temporally arranged into cycles of four major exodus waves (2.0–1.6 Ma, 1.4–1.2 Ma, 1.0–0.8 Ma, and 0.6–0.1 Ma) controlled by climatic and environmental changes).

Climate in Relation to the Evolution of Ontogeny

Heterochrony Pulses: Parallel Developmental Responses to Common Environmental Causes

The term heterochrony has been applied to both ecophenotypic and evolutionary changes in the rates and timing of ontogenetic events (Gould 1977). The same kind of heterochronic phenotype, *H*, commonly appears independently in different parts of a given monophyletic group in association with the same kind of environmental condition, *E*, and variously as an ecophenotype (i.e., reversible in later generations not faced by *E*) or as a phenotype, the expression of which is genetically fixed (or at least more constrained under varying conditions). An example is relative reduction of limb length in colder environments, an aspect of Allen's Rule (Allen 1877: mammalian extremities are reduced relative to body size in cooler climates). Not only the environmental association with *E* but also the growth patterns tend to be similar between the independent occurrences of such a phenotype *H* in a clade (e.g., Gould 1977a; Wake and Larson 1987; Vrba 1998b). It appears that certain kinds of heterochrony are more likely than others under particular environmental changes. Each heterochrony response starts off from the ancestral ontogenetic trajectory for that character, and this inheritance imparts limits and direction on what can grow and evolve. To the extent that aspects of ontogeny are shared by common inheritance between related species and across larger taxonomic groups, similar kinds of heterochrony will evolve independently in related lineages faced by the same environmental change. A summary and extension of the above is given in the following two statements (Vrba 2004, 2005):

1. Similar environmental changes elicit similar heterochronies in parallel, potentially in numerous lineages across large phylogenetic groups. Such heterochrony often involves change in body size and may be accompanied by large-scale phenotypic reorganization (Arnold et al. 1989; Vrba 1998b), such that the parallel heterochronies involve concerted evolution of suites of linked characters and "shuffling" among body proportions.
2. At times of widespread climatic change, diverse lineages may show parallel changes in size and in similar kinds of heterochrony associated in time and consistently with the climatic change – a "heterochrony pulse." "Pulse" here does not imply that the lineages responded in unison in a short time, but only that the events are significantly concentrated in time.

I will mention one particular category of heterochrony, which is associated with body size increase by prolongation of growth and which is a common mammalian response to colder temperatures. It is of special interest in the Plio-Pleistocene context of net global cooling, and it appears to have affected many African mammals including some evolutionary changes in *Homo*.

Cooling and Body Size Increase. Many species with FADs during times of cooling and aridification were larger than their ancestral phenotypes (as cladistically inferred). For example, Vrba (2004) tested H_0 that size changes across lineages are randomly distributed in time in the Alcelaphini (wildebeests, etc.) and Reduncini (waterbuck, etc.), which together comprise 63 recorded species over the past 5 Ma with a body weight range of ca. 20–250 kg. The result of significant peaks in size increase 3.0–2.5 Ma and 1.0–0.5 Ma ago, two periods with strong cooling, is consistent with Bergmann's Rule (1846: larger bodies are associated with colder temperature). While exceptions have been noted, in general, the predictions are upheld in living mammals (Ashton et al. 2000; Meiri and Dayan 2003) including in humans (Baker 1988) and in fossil mammals (Davis 1981; Kurten 1959; Heintz and Garutt 1965). To evaluate the claim that climate-associated heterochrony can involve extensive rearrangement – or "shuffling" – among body proportions, with parallel changes across related lineages, consider the example of Bergmann's Rule. Bodies can become enlarged by faster growth relative to the plesiomorphic (or directly ancestral) ontogeny, by prolongation of growth time, or by a combination of both, and the influential factors may include temperature change itself or one of the attendant environmental changes (such as seasonal changes in food and water availability, e.g., Guthrie 1984; Barnosky 1986). Such changes in growth mode are expected to result in rearrangement of body proportions. This is especially true of growth prolongation which is prevalent among Bergmann cases for which there are growth studies. For instance, many African tropical ungulates have shorter growth periods to smaller size in warm lowlands, while their close relatives at higher altitudes and/or latitudes grow for longer and become larger. The example of polymorphism in the African buffalo was noted earlier: *Syncerus caffer caffer* is much larger (up to 810 kg), grows for longer, and lives at higher latitudes and/or altitudes always near grassland, while the smaller and plesiomorphic phenotype *S. c. nanus* (up to 320 kg) with a shorter growth period lives in warmer, more forested regions.

Body Size Increase and "Shuffling" Among Body Proportions. Consider what is expected under the simplest way in which growth prolongation could occur: namely, if all ancestral growth phases for a character become proportionally prolonged (or extended in time by a constant factor) while maintaining the ancestral number of growth phases and the ancestral growth rates for respective phases (Vrba 1998b: Fig. 1). Let us call that simple proportional growth prolongation. Characters in the same organism have differing growth profiles, in terms of growth timing and rate in relation to age and body weight (e.g., Falkner and Tanner 1986), and character growth typically occurs in distinct phases in each of which character change is nonlinear with respect to age (Koops 1986). We can distinguish two major types of heterochrony and associated allometric growth under growth prolongation: (A) in type A heterochrony, characters which grow with net negative allometry with respect to age and body size will become reduced relative to body size in the adult stage of the prolonged descendant ontogeny (even if no other growth parameter changes) and paedomorphic in that the descendant adult resembles the ancestral juvenile. A probable example is the character evolution by Allen's Rule (Vrba 1998b, 2004) which is upheld in modern humans (Baker 1988). The persistence of Allen's Rule in modern biology supports the general hypothesis of similar changes in body proportions across lineages, which share inherited developmental responses to common environmental causes. (B) In type B heterochrony, characters which grow with net positive allometry become relatively enlarged. This mode, particularly by prolongation of a positively allometric late growth phase, may be how the hypermorphosed antlers of the giant Irish elk evolved (Gould 1974) and how exaggerated secondary sexual characters in enlarged bodies commonly evolve (Vrba 1998b). As growth trajectories become prolonged, some characters become relatively reduced and others enlarged, with potentially extensive rearrangement among body proportions and substantial evolutionary novelty (Vrba 1998b: Fig. 1). Type B heterochrony can also result from prolongation of positively allometric *early* growth, in which case the descendant structure is relatively enlarged and paedomorphic. An example is provided by the enlarged hind-feet of the bipedal, saltatory rodents during times of cooling (section "Climate in Relation to Habitats and Adaptations of Hominins"). If the growth of rodents, the juveniles of which in general have relatively large hind-feet

(Hafner and Hafner 1988), is prolonged, a descendant adult with enlarged hind-feet is predicted. Evidence for at least some taxa is consistent with this; e.g., bipedal Kangaroo rats, *Dipodomys*, which inhabit semiarid to arid regions in North America, have longer growth periods and are hypermorphosed in some characters – yet paedomorphosed in others – relative to the ancestral ontogeny (Hafner and Hafner 1988). As noted earlier, the bipedal forms share suites of characters in a characteristic body plan that is today strongly associated with open, arid habitats and has appeared independently in 24 genera in 8 families (Hafner and Hafner 1988). I do not know how many of the 24 instances of parallel evolution involved growth prolongation. But I suggest that at least some of these appearances of suites of integrated character complexes exemplify coordinated morphological changes, by growth prolongation, within and between lineages in response to a common climatic cause. This case illustrates that evolution by growth prolongation, as it acts on characters with different nonlinear growth profiles in the same body plan, can result in a "shuffling" of body proportions. Substantial novelty in form can result and also in function as in these rodents which can jump to a height that is from 4 to 25 times their body length. I next discuss another example of type B heterochrony with prolongation of positively allometric early growth, namely, encephalization.

Heterochrony and Brain Evolution. I applied statistical models for multiphasic growth to data on living human and common chimpanzee brain weights at ages since conception to test the hypothesis that encephalization of the human brain occurred by simple proportional growth prolongation (Vrba 1998b). Specifically, I wanted to know whether prolongation of the fetal growth phases, with strongly positive allometric growth, could account for most of the observed EQ increase. The results supported the hypothesis and imply that gross brain weight increase toward humans required change in only one growth parameter: prolongation of the nonlinear ancestral growth phases. In mammals, in general, simple growth prolongation is predicted to result in encephalization, as all mammalian brains complete a large proportion of their total growth rapidly early in ontogeny (Count 1947; Holt et al. 1975). A positive correlation of EQ with more open, seasonally cooler and drier environments has been noted in diverse mammals (Vrba 2004; e.g., in living African bovids this association is supported by comparison of the habitat preferences of the species with Oboussier's 1979 results for their EQ variation). This raises the hypothesis that there were past "encephalization pulses," across many mammalian lineages, in response to cooling over particular intervals (Vrba 1998b).

Conclusion

Environmental stimuli have influenced the evolution of hominins and other mammals at the levels of ontogeny, organismal adaptation, and speciation. From a time a few decades ago, when any proposal that climatic change is causally linked to speciation of hominins and other mammals was subjected to much doubt and even derision, there is now substantial convergence of opinion that such a linkage is real.

The climatic influence on hominin adaptation has received most attention, and some agreement has also emerged in this area: successive cooling trends since the late Pliocene were associated with the earliest evidence of – and probably initiated – the "hypermasticatory trend" in *Paranthropus* (ca. 2.6 Ma) and its later exaggeration ca 2.3 Ma, stone tools and their use to butcher carcasses (ca. 2.6–2.5 Ma), the Early Pleistocene expansion of tool kits, increased mobility by the Plio-Pleistocene interface and commitment to long-range bipedalism (ca. 1.6 Ma) in *Homo*, and significant brain expansion near 2 Ma and also since 600 Ka ago. There is some consensus that encephalization and culture in *Homo* represent generalist adaptations which conferred a more flexible and expanded use of resources (Vrba 1985a, 1988, 1989a; Potts 1998a; Wood and Strait 2003). It now seems likely that the masticatory features of *Paranthropus*, while adaptations for consuming tough or gritty foods, had the effect of broadening, not narrowing, the range of food items consumed and allowed these forms to subsist in varied environments (Wood and Strait 2003). There is less agreement on environmental stimuli of the onset of bipedalism, particularly on whether the vegetational habitats of the earliest bipedal hominins were forest to dense woodland or more open. I discussed why, even if the hominin ancestor and its bipedal descendant species both live(d) in forest, this does not necessarily mean that climatic change did not bring about speciation.

Far less work has been done on the issue of environmental causes of hominin speciation. A brief summary of the current status is as follows: in terms of theory, the expectation that allopatric speciation predominates, particularly in hominins and other large mammals, is consistent with the weight of available evidence. It would take special pleading to argue that hominins are exceptions. If allopatric speciation predominates, then so must physical initiation of speciation predominate. Most, and possibly all, of the hominin FADs either coincide with or fall very close to one of the major cooling trends. While taphonomic factors and chance may have contributed to this pattern, it does leave intact the hypothesis of climatic cause of hominin speciation. Also, on cladistic grounds, some speciation events must be closely associated with climatic change in hominins (Kimbel 1995) and other African mammals (Vrba 1995c).

Environmental stimuli of ontogenetic evolution have hardly been studied in our field. I discussed the "heterochrony pulse hypothesis": the generative properties shared among lineages can result not only in coherence of morphological changes but also in a strongly nonrandom timing of heterochrony events, as diverse lineages respond in parallel by similar kinds of heterochrony to the same environmental changes. This has not yet been tested. Of particular interest in the present Late Neogene climatic context is heterochrony involving body enlargement by prolongation of growth, because it is associated with colder (at least seasonally colder) temperatures (Bergmann's Rule, upheld in modern humans, Baker 1988). I have discussed some examples, including encephalization as a result of growth prolongation, in hominins and other mammals, and suggested that there were past "encephalization pulses," across many mammalian lineages, in response to cooling trends over particular intervals, such as during the onset and later intensification of the modern ice age.

In our field, one sometimes regrets (at least I do) that conclusive answers, such as those that emerge from some experiments of physical scientists, are so difficult to achieve. Hypotheses on the subject of environmental causes of hominin and other biotic evolution are difficult to test because the data come from different subdisciplines, each with its own set of biases, errors, and ambiguities. As a result, debates tend to continue interminably. While we have a long way to go, on the positive side, we can take heart in the simple fact that we are, so to speak, in a "growth industry": while many aspects of life are deteriorating, the fossil record with its associated geological information is constantly improving. Thus, there is an excellent expectation of decisive future progress on some of the unresolved issues. In my view, the results to date already offer support for the notion that common rules give qualitative and temporal coherence to the evolutionary responses across many mammalian – including hominin – lineages. These common rules arise from the regularities of physical change and from attributes of organismal ontogenies and phenotypes and species that are widely shared by common inheritance. The evidence implies closer linkages between the physical and biotic dynamics on earth than has traditionally been acknowledged. This perspective contrasts with the neoDarwinian view that selection of small-step random mutations is the vastly predominant evolutionary cause, with the implication that each evolutionary advance is to a larger extent an independent piece of history. Evolution is more rule bound than that, and our evolution is no exception.

Cross-References

- ▶ Contribution of Stable Light Isotopes to Paleoenvironmental Reconstruction
- ▶ Geological Background of Early Hominid Sites in Africa
- ▶ Paleoecology: An Adequate Window on the Past?
- ▶ Patterns of Diversification and Extinction
- ▶ Species Concepts and Speciation: Facts and Fantasies
- ▶ The Evolution of the Hominid Brain
- ▶ The Ontogeny-Phylogeny Nexus in a Nutshell: Implications for Primatology and Paleoanthropology
- ▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments
- ▶ The Species and Diversity of Australopiths

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