

African climate change and faunal evolution during the Pliocene–Pleistocene

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Abstract

Environmental theories of African faunal evolution state that important evolutionary changes during the Pliocene–Pleistocene interval (the last ca. 5.3 million years) were mediated by changes in African climate or shifts in climate variability. Marine sediment sequences demonstrate that subtropical African climate periodically oscillated between markedly wetter and drier conditions, paced by earth orbital variations, with evidence for step-like (± 0.2 Ma) increases in African climate variability and aridity near 2.8 Ma, 1.7 Ma, and 1.0 Ma, coincident with the onset and intensification of high-latitude glacial cycles. Analysis of the best dated and most complete African mammal fossil databases indicates African faunal assemblage and, perhaps, speciation changes during the Pliocene–Pleistocene, suggesting more varied and open habitats at 2.9–2.4 Ma and after 1.8 Ma. These intervals correspond to key junctures in early hominid evolution, including the emergence of our genus *Homo*. Pliocene–Pleistocene shifts in African climate, vegetation, and faunal assemblages thus appear to be roughly contemporary, although detailed comparisons are hampered by sampling gaps, dating uncertainties, and preservational biases in the fossil record. Further study of possible relations between African faunal and climatic change will benefit from the accelerating pace of important new fossil discoveries, emerging molecular biomarker methods for reconstructing African paleovegetation changes, tephra correlations between terrestrial and marine sequences, as well as continuing collaborations between the paleoclimatic and paleoanthropological communities.

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1. Introduction

Recent extraordinary fossil discoveries, advances in the analysis of extant fossil collections, and the emergence of detailed paleoclimatic records have focused new attention on the possible role that changes in African climate may have had in the evolutionary history of African mammalian

fauna spanning the last 5–6 million years. The basic premise is that large-scale shifts in climate alter the ecological composition of a landscape which, in turn, present specific faunal adaptation or speciation pressures leading to genetic selection and innovation.

This review explores the African faunal and paleoclimatic evidence which constrains current environmental hypotheses of African faunal evolution. Still hotly debated, these hypotheses now draw upon a wealth of new fossil and paleocli-

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matic evidence which have been used to explore possible temporal and causal relationships between known changes in climate and observed changes in faunal diversity and adaptation. Beginning with an overview of some leading climate–evolution hypotheses, this review discusses recent developments in what is known about the Pliocene–Pleistocene development of African paleoclimates based on terrestrial and marine paleoclimatic data. The hominid fossil record of the human family tree is now viewed to be considerably more complex than previously thought [1], although key transitional intervals of evolutionary and behavioral change are apparent. Advances in the analysis of large fossil mammal databases from collections in Kenya, Tanzania, and Ethiopia have led to new perspectives on the timing, signatures, and possible causes of key steps in African faunal evolution and assemblage changes. Taken together, these new data narrow the range of possible scenarios whereby changes in climate may have led to changes in fauna.

2. African climate – faunal evolution hypotheses

Natural selection, the process by which new adaptive structures evolve and persist, is viewed as the primary mechanism by which organisms change in relation to their environment. Long-term shifts in climate and secular shifts in climate variability are two separate ecological signals which can establish natural selection opportunities. Most environmental hypotheses of African faunal evolution are ‘habitat-specific’ [2] in that they consider faunal adaptations to a specific environment, most commonly the emergence of grassland savannah which occurred after the late Miocene [3–5]. The ‘variability selection’ hypothesis [2,6,7] incorporates observations about patterns of African paleoclimatic variability as recorded by deep-sea sediments, and it emphasizes the importance of climatic instability as a mechanism for natural selection. A review article by Richard Potts [2] presents a superb overview of the historical contexts, and faunal and ecological evidence for many environmental hypotheses of African faunal evolution.

2.1. ‘Habitat-specific’ hypotheses

The savannah hypothesis is perhaps the best known and most widely studied of the habitat-specific hypotheses of African faunal evolution [8–11]. In an early and unmistakably habitat-specific account of human evolution, Raymond Dart [8] posited that key human traits such as bipedality and larger brains were consequences of life on the open savannah. It was very provocative and influential (it is still found in some textbooks), but it was largely unconstrained by data as the fossil record at that time consisted of very few specimens with little paleoclimatic context. Current evidence indicates that bipedality was established millions of years before the widespread expansion of savannah grasslands [3,7,12–14].

Current interpretations of the savannah hypothesis state that the evolution of African mammalian fauna, including early hominids, was primarily attributable to the step-like development of cooler and drier and more open conditions which occurred since the late Miocene. The mid-Pliocene aridification shift near 3.2–2.6 Ma [15–17], in particular, is viewed to have favored the evolution of arid-adapted fauna and to have influenced early hominid evolution and behavior [15,18–26].

The turnover pulse hypothesis is one variant of the savannah hypothesis initially proposed by Elisabeth Vrba [21,27,28]. The essence of this view is that focused bursts of biotic change (or ‘turnover’, quantified in terms of clustered first- and/or last-appearance datums) were initiated by fundamental shifts in African climate which occurred roughly near 2.8 Ma, 1.8 Ma, and 1.0 Ma [15,28–31]. An analysis of fossil bovid (antelope) evolution from the largest African collections revealed clusters of first- and last-appearance datums which occurred near 2.7–2.5 Ma, with secondary clusters near ca. 1.8 Ma and ca. 0.7 Ma [21]. Many of the first appearances between 3.0 and 2.5 Ma were grazing species, supporting the view that the faunal changes were linked to aridity and expanding grasslands [21,26,32]. Although elegant and influential, the turnover pulse hypothesis has also been challenged recently (see Section 4.1) [33–35].

Other habitat-specific hypotheses argue for the

adaptive importance of environments other than open grasslands. Based on fossil pollen records from a 3.3–3.0 Ma fossil hominid site in South Africa, Rayner and others have alternatively proposed the forest hypothesis [36] which argues that closed vegetation, not savannah, was the adaptive environment for early bipeds. Blumenschine [37] has proposed that early tool-making hominids exploited the resources of grassland–woodland mosaic zones.

2.2. *The variability selection hypothesis*

This view of African faunal change accommodates one of the more obvious yet also curious features of African faunal and paleoclimatic records [2,6]. Individual fossil hominid and other mammal lineages typically persisted over long durations (10^5 – 10^6 years) yet they are preserved within sediment sequences which indicate much shorter-term (10^3 – 10^4 year) alternations between wetter and drier paleoenvironments [38,39]. Similarly, marine records of African paleoclimatic variability demonstrate that faunal lineages must have survived repeated alternations of wetter and drier periods paced by earth orbital variations of the African monsoon [15,17].

The ‘variability selection’ hypothesis emphasizes the importance of secular changes in climatic variability (amplitudes and durations of departures from the mean climatic state) on faunal adaptation, selection, and evolution [2,6]. In contrast to habitat-specific hypotheses, variability selection calls upon environmental instability (such as changes in the amplitudes and durations of orbital-scale wet–dry cycle amplitudes) as agents for introducing genetic variance, natural selection, and faunal innovation. Variability selection would argue that the largest faunal speciation and innovation pressures should occur during those periods when the amplitudes of climate variability changed markedly. This hypothesis proposes that African hominids and other fauna would have occupied increasingly diverse habitats following increases in paleoclimatic variability [2]. Many of the largest African faunal evolution events occurred when there were increases in the amplitudes of paleoclimatic variability [2].

3. African paleoclimate

3.1. *Subtropical North African climate*

North African vegetation zones range impressively from tropical rainforests to hyperarid subtropical deserts (Fig. 1a). The tremendous seasonal range in North African rainfall is a consequence of the seasonal migration of the intertropical convergence zone associated with the African monsoon. During boreal summer, sensible heating over the North African land surface centered near 20°N draws moist maritime air from the equatorial Atlantic into western and central subtropical Africa [40] which nourishes the grassland and woodland savannahs (Fig. 1b). East African summer rainfall is also related to the westerly airstream of the African monsoon, but is highly variable due in part to topographic rainshadow effects [41]. The Kenyan and Ethiopian Highlands orographically capture some of this moisture and this summer monsoonal runoff feeds the many subtropical rivers draining East Africa such as the Nile and Omo rivers. During boreal winter, the African and Asian landmasses cool relative to adjacent oceans and the regional atmospheric circulation reverses; dry and variable northeast trade winds predominate and ocean temperatures warm off Somalia and Arabia (Fig. 1c).

The large seasonality in rainfall promotes the production and transport of atmospheric mineral dust which is exported to the adjacent Atlantic and NW Indian oceans. Interannual to multidecadal changes in West African dust export to the Atlantic are very closely related to changes in subtropical African summer rainfall [42], which in turn have been linked to tropical Atlantic sea-surface temperature (SST) anomalies [43]. A prominent summer dust plume off West Africa is carried at mid-tropospheric levels (700 mbar) by the African Easterly Jet and its load is mainly derived from western Saharan sources (Fig. 1b). The winter African dust plume originates from seasonally dry sub-Saharan and Sahelian soils which are carried by northeast trade winds (Fig. 1c). Summer dust plumes off Arabia and northeast Africa (Fig. 1b) are associated with Indian monsoon surface winds and they transport abun-

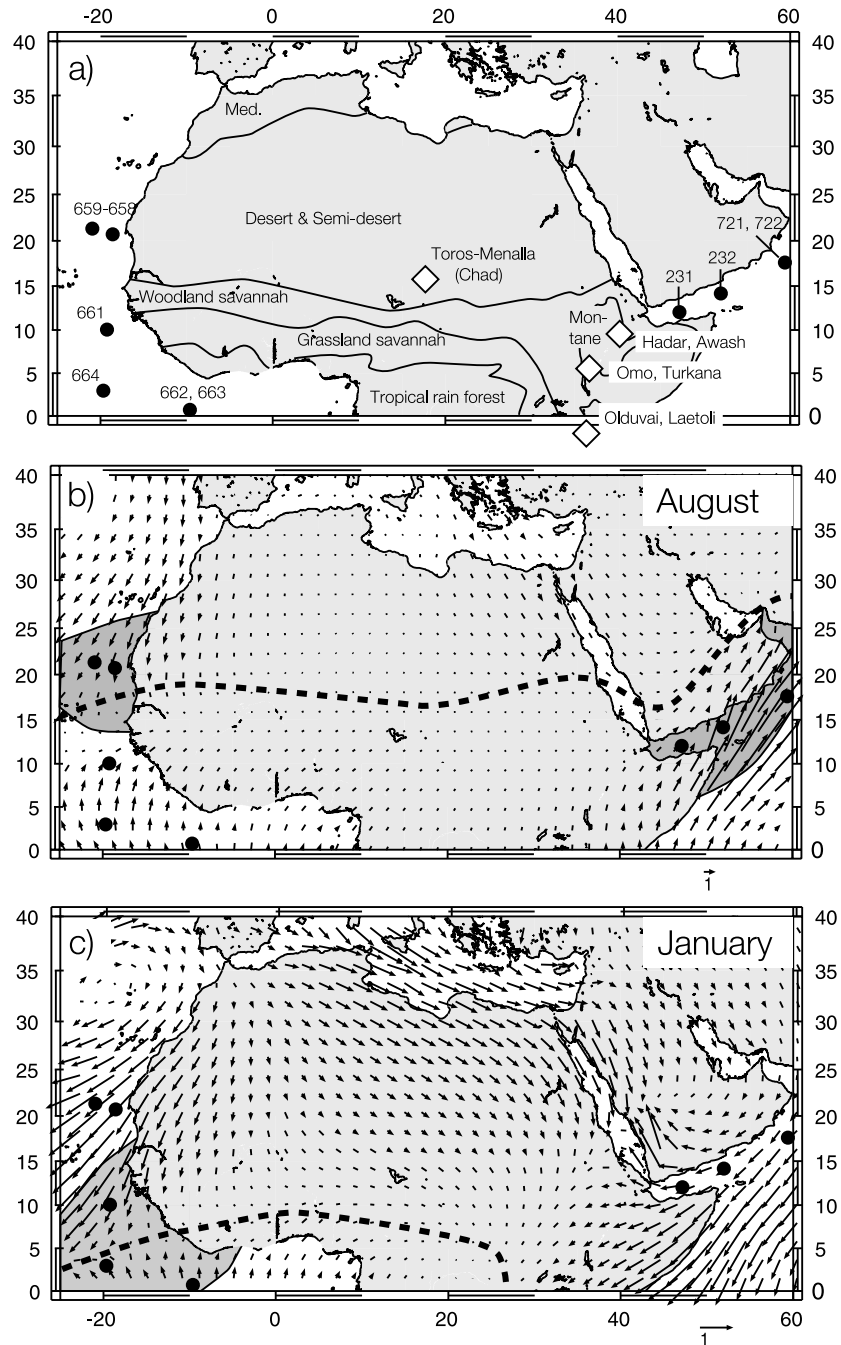


Fig. 1. (a) Regional map of North African vegetation zones, locations of DSDP and ODP drill sites (filled circles), and locations of selected African mammal fossil localities (open diamonds). (b) Boreal summer (August) surface wind stress (unit vector = 1 dyne/cm²), intertropical convergence zone (ITCZ, heavy dashed line) location, and boundaries of seasonal tropospheric dust plumes off NW Africa and NE Africa/Arabia. Dust plume contours were derived from haze frequency data [46]. (c) Boreal winter (January) surface wind stress (unit vector = 1 dyne/cm²), ITCZ location, and boundary of the seasonal tropospheric dust plume off NW Africa.

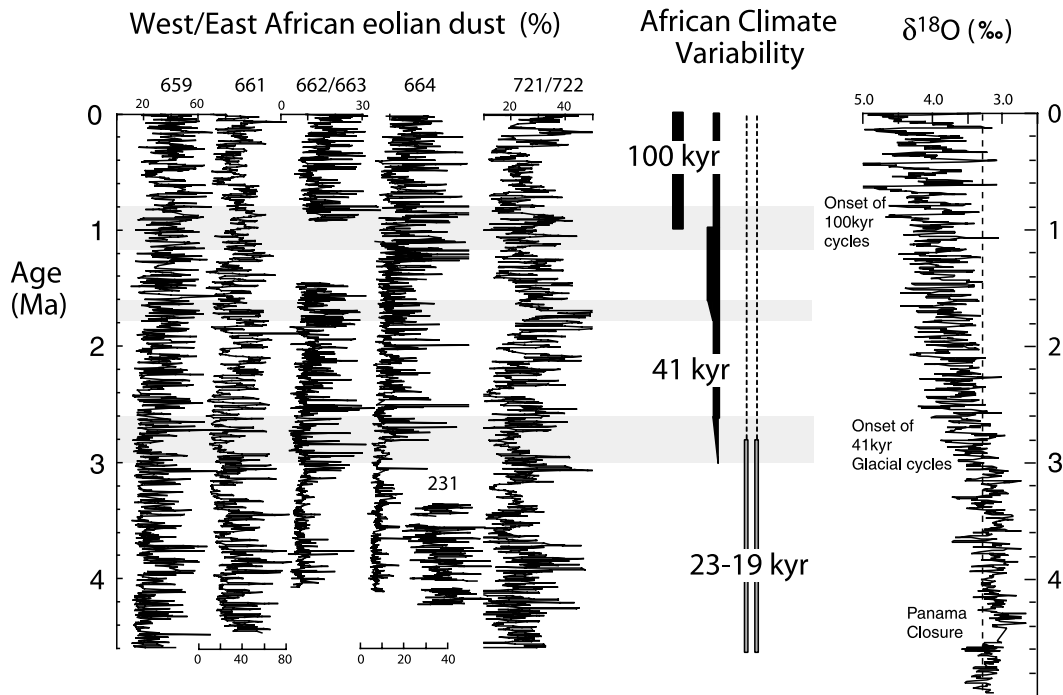


Fig. 2. Pliocene–Pleistocene records of eolian dust deposition at seven DSDP/ODP sites off western and eastern subtropical Africa [15] (Fig. 1). Terrigenous sedimentation at these sites is dominated by wind-borne eolian dust contributions from source areas in the Sahara/Sahel regions off West Africa, or source areas in the Arabian peninsula and northeast Africa. The terrigenous percentage records were determined by chemical removal of carbonate, opal, and organic fractions and most records were constrained by detailed oxygen isotopic stratigraphies [15,30,31,56]. The records collectively document progressive shifts in African climate variability and increasing aridity after 3.0–2.6 Ma, 1.8–1.6 Ma, and 1.2–0.8 Ma. These African aridity shifts were coincident with the onset and subsequent amplification of high-latitude glacial cycles [15,30,31,56]. The composite benthic foraminifer oxygen isotope record illustrates the evolution of high-latitude climate over the study interval [15,146,147].

dant mineral dust to the Arabian Sea and the Gulf of Aden [44–46]. Sediment trap and mineralogic studies demonstrate that wind-borne detritus from these source areas comprises the dominant source of terrigenous sediment to the eastern equatorial Atlantic and the Arabian Sea [45,46].

3.2. Marine paleoclimatic records

Marine sediments accumulating off the western and eastern margins of subtropical North Africa have provided some of the most compelling evidence for recurrent arid–humid climate cycles and progressive step-like increases in African aridity during the late Neogene (last ca. 5 Myr). These records document how African climate varied during a period of profound global climate shifts associated with the gradual onset of high-latitude

glacial cycles at 3.2–2.6 Ma which followed the isolation of the Atlantic basin resulting from the closure of the isthmus of Panama after 4.4–4.6 Ma [47] (Fig. 2). Pliocene–Pleistocene cooling at high latitudes occurred as a series of steps commencing with the onset of glacial ice rafting and modest 41 kyr glacial cycles after ca. 2.8 Ma, a shift toward cooler conditions and higher-amplitude 41 kyr cycles after ca. 1.8–1.6 Ma, and a pronounced shift toward still larger 100 kyr glacial cycles after ca. 1.2–0.8 Ma [48–51] (Fig. 2).

3.2.1. Patterns of subtropical African paleoclimatic variability

Marine sediment records of Pliocene–Pleistocene eolian export from West and East subtropical Africa (Fig. 1) reveal several consistent patterns of variability (Fig. 2) [15].

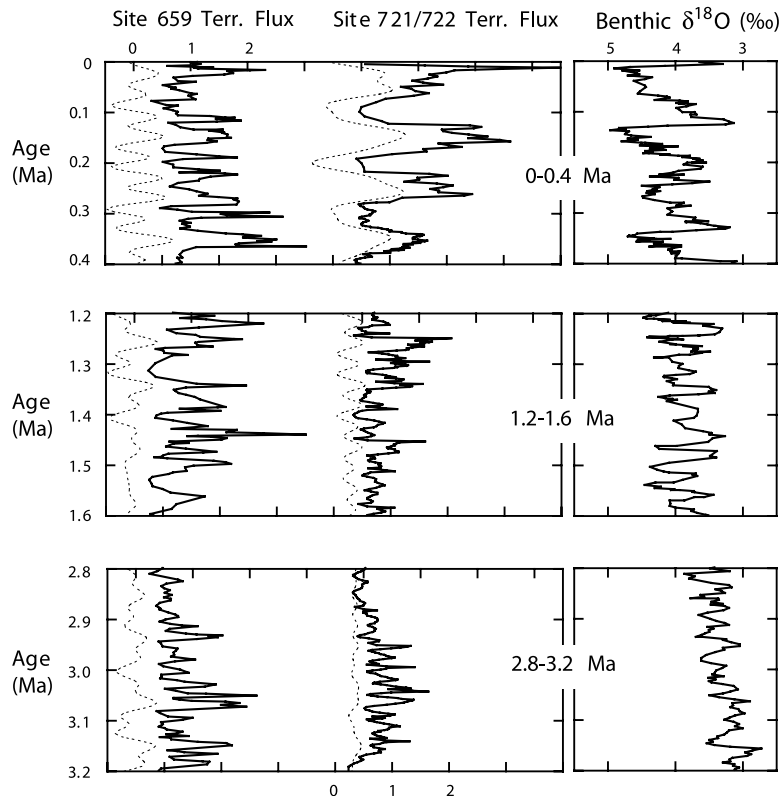


Fig. 3. Detail of terrigenous input (flux) variability at West African Site 659 and East African Site 721/722 spanning three intervals with differing patterns of eolian variability. The terrigenous (eolian) flux records (in units of $\text{g}/\text{cm}^2/\text{kyr}$) were calculated at each site as the product of terrigenous percentage data (Fig. 2), and interval sedimentation rate and dry bulk density data [15,30,31,54,56]. Dashed curves in each panel show the combined 100 kyr and 41 kyr period bandpass filters of the terrigenous flux series to illustrate changes in the amplitude and dominant period of eolian supply during the Pliocene–Pleistocene. Note the predominance of precessional (23–19 kyr) variability for the 3.2–2.8 Ma interval, whereas larger 41 kyr cycles dominate the 1.6–1.2 Ma interval, and still larger 100 kyr and 41 kyr cycles dominate the 0.4–0 Ma interval (particularly at Site 721/722). Long-term trends towards increased eolian flux variability are most evident at Site 721/722, although they are also apparent at West African Sites 659, 662, and 664 [15,30,31,54,56].

1. Orbital-scale African climate variability persisted throughout the entire interval, extending in some cases into the Miocene and Oligocene [52,53].
2. The onset of large-amplitude African aridity cycles was closely linked to the onset and amplification of high-latitude glacial cycles [15,30,31,54–57].
3. Eolian concentration and supply (flux) increased gradually after 2.8 Ma [30,31,54,55].
4. Step-like shifts in the amplitude and period of eolian variability occurred at 2.8 (± 0.2) Ma, 1.7 (± 0.1) Ma, and 1.0 (± 0.2) Ma [15,30,31].
5. Evidence for 10^4 – 10^5 year ‘packets’ of high-

and low-amplitude paleoclimatic variability which were paced by orbital eccentricity [15,30].

The marine record of African climate variability is perhaps best described as a succession of wet–dry cycles with a long-term shifts toward drier conditions, punctuated by step-like shifts in characteristic periodicity and amplitude. Prior to 2.8 Ma subtropical African climate varied at the 23–19 kyr period (Figs. 2 and 3) which has been interpreted to reflect African monsoonal variability resulting from low-latitude (precessional) insolation forcing of monsoonal climate [15]. After 2.8 (± 0.2) Ma, African climate varied primarily at

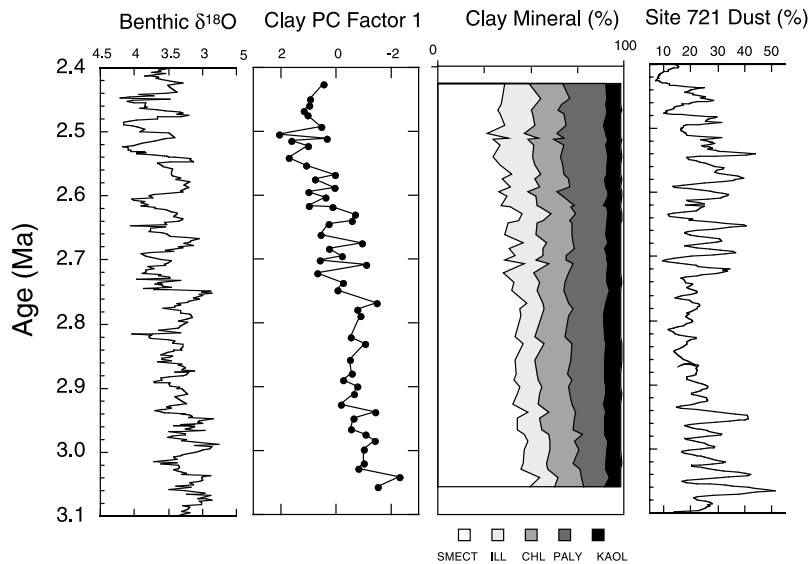


Fig. 4. Clay mineral assemblage variations in the Arabian Sea are used to reconstruct past variations in regional climate by taking advantage of the very different source vectors of specific clay minerals [148–150]. Presently, smectite derives from weathering and runoff of the Deccan traps of western India, and chlorite contributions similarly reflect northern source clay minerals associated with Indus River drainage. In contrast, variations in the fibrous Mg-rich clay mineral palygorskite reflect climate changes in southern source regions in Somalia and Arabia, where it forms in arid, alkaline environments [149]. The clay mineral percentage data [150] reveal a trend toward increasing palygorskite and illite, and decreasing smectite abundances after 2.8 Ma which are interpreted to reflect enhanced aridity (or transport) from source areas in Somalia and southern Arabia [149,150]. This shift is apparent in first principal component extracted from the clay mineral abundance matrix (PCA factor 1, 53% of variance).

the longer 41 kyr period and the amplitude of these cycles increased again after 1.7 (± 0.1) Ma. Eolian variability shifted towards longer and larger-amplitude 100 kyr cycles after 1.0 (± 0.2) Ma. These shifts in African eolian variability were synchronous with shifts in the onset and amplification of high-latitude ice sheets and cooling of the subpolar oceans [49,58], suggesting a coupling between high- and low-latitude climates after the onset of glaciation near 2.8 Ma [15,30,31,56] (Figs. 2 and 3). Three separate 0.4 Myr intervals from West African Site 659 [30] and East African Site 721/722 [15] are shown in Fig. 3 to illustrate these shifts in eolian variability.

African climate sensitivity to high-latitude glacial boundary conditions has been examined using general circulation model experiments [59–63] which indicate shifts to cooler, drier African conditions during glacial extrema. A detailed Pliocene–Pleistocene pollen record from Site 658 documents a progressive expansion of xeric vege-

tation and greater variability after ca. 3 Ma [17]. Changes in clay mineral assemblages at Site 721/722 similarly indicate increases in NE African aridity after 2.8 Ma (Fig. 4). Based on analysis of the terrigenous (eolian) grain size record over the last 3.5 Myr at Site 722, Clemens and others [31] additionally documented discrete shifts in the intensity and phase of the Indian monsoon at ca. 2.6 Ma, 1.7 Ma, and 1.2 Ma, and 0.6 Ma.

Most eolian concentration records display long-term trends toward greater dust concentrations after 2.8 Ma (Fig. 2), and this is particularly evident in calculated dust flux records [15,30,31,56]. A post-2.8 Ma shift toward enhanced eolian variability is most dramatic at Sites 662, 663, and 664 which are furthest from dust source areas (Fig. 1a). In addition to enhanced source area aridity, the abrupt dust increases at these most distal sites are likely reflecting glacial trade wind invigoration [17,64–72] and/or a southward shift of the inter-tropical convergence zone [73,74]. The ultimate

cause for the onset of glaciations and African aridity after ca. 2.8 Ma remains a mystery, although several plausible mechanisms have been proposed [50,75–78].

At Arabian Sea Site 721/722, eolian grain size measurements document gradual weakening of the monsoonal dust-transporting winds after ca. 2.8 Ma, whereas the fluxes of eolian sediment to this same site increased markedly over the same time [31]. Thus, for East Africa and Arabia the post-2.8 Ma increase in eolian supply most likely reflects real increases in source area aridity. These sites also indicate an interval of pronounced aridity between 1.6 and 1.8 Ma which is not expressed at other locations (Fig. 2), perhaps suggesting a regionally specific signal. A pronounced shift toward more open conditions in East Africa at this time is indicated from stable isotopic records of soil carbonates recovered from several hominid fossil localities [3,4].

The eolian records exhibit ‘variability packets’ – long-term (10^4 – 10^5 year) modulations in the amplitudes of African paleoclimatic variability. These modulations have been attributed to orbital eccentricity modulation of Earth precession which regulates seasonal insolation and, consequently, the strength of the African and Indian monsoons [15,30,31]. These eccentricity-modulated ‘variability packets’ represent 10^4 – 10^5 year intervals of exceptionally high- or low-amplitude paleoclimatic variability, and are evident in both West and East African eolian records (Fig. 5). The impact of these paleoclimatic variability packets on African faunal evolution remains to be investigated, but at least one view, the variability selection hypothesis, cites the potential importance of such extended periods of paleoclimatic stability and instability to faunal adaptation and evolution [6,7].

3.2.2. On the fundamental pacing of African paleoclimatic variability

The fundamental pacing of African climate remains curiously unresolved [66]. From a marine sediment perspective there is abundant evidence that once high-latitude ice sheets became sufficiently large to sustain glacial–interglacial oscillations after 2.8 Ma, African climate covaried with

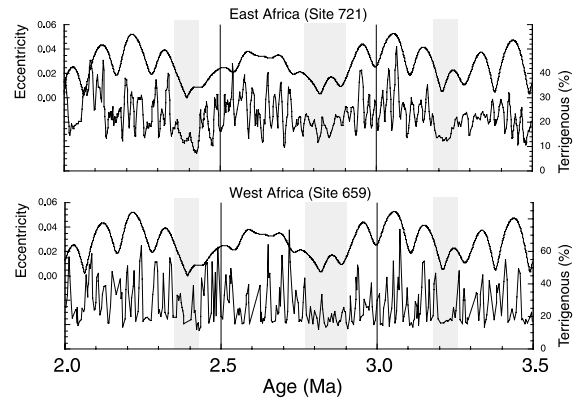


Fig. 5. Evidence for high- and low-amplitude African climate ‘variability packets’ from West and East African Sites 659 and 721/722 [15,30]. African paleoclimate variability over this interval was strongly regulated by orbital precession which is modulated by orbital eccentricity (shown). Prolonged (10^4 – 10^5 year) intervals of exceptionally high- or low-amplitude paleoclimate variability are apparent off both margins of subtropical Africa. Highest variability occurs during periods of maximum orbital eccentricity (e) when modulation of the precession index ($I = e \sin(\omega)$) is greatest [63,151].

these high-latitude climate cycles at the characteristic 41 kyr and 100 kyr periodicities. However, the Pliocene–Pleistocene succession of sapropel layers in the Mediterranean Sea suggests that orbital precession was the fundamental tempo of African paleoclimatic changes [79–81]. These dark, organic-rich sapropel layers were deposited during African humid periods when enhanced monsoonal rainfall and Nile River runoff led to increased Mediterranean stratification and reduced ventilation of its deep eastern basins [79,82]. Dramatic cliffside exposures of uplifted Pliocene–Pleistocene marine sediments in southern Sicily and Calabria (Fig. 6) and sediment cores from eastern Mediterranean basins confirm the predominant influence of orbital precession on African climate since at least the late Miocene to the present [79–81,83].

It is possible to reconcile these two views by acknowledging that precession was the fundamental driver of African monsoonal climate throughout the late Neogene, but that high-latitude glacial cooling and drying effects were superimposed on this signal only after 2.8 Ma [15,56]. The ‘glacial tempo’ apparent in the marine dust and pol-



Fig. 6. Photograph of late Miocene (9.3–8.4 Ma) sapropel bedding cycles from the Gibliscemi A section in south central Sicily [53,83]. The darker strata are organic-rich sapropel layers which were deposited during African humid periods when enhanced monsoonal rainfall and Nile River runoff led to increased Mediterranean stratification and reduced ventilation of its deep eastern basins [79,82]. The regular bundling of sapropel layers into groups of three to four cycles reflects the 100 kyr eccentricity modulation of the precessional African humid periods. The predominant influence of orbital precession and eccentricity on African monsoonal rainfall persists throughout the Pliocene and Pleistocene [81,152], although there is evidence for some obliquity forcing as well [153]. Photograph courtesy of Frits Hilgen and Utrecht research group on astronomical climate forcing and timescales.

len records thus reflects glacial-stage increases in source area aridity and/or increases in the strength of the transporting winds [17,56,66,84], both of which are known subtropical climate responses to imposed glacial boundary conditions in climate models [15,59,61]. Prior to 2.8 Ma, the marine sediment eolian records and the sapropel records tell a consistent story, namely that changes in African monsoonal climate were paced mainly by precession [15] (e.g. Fig. 5), as would be expected in the absence of large ice sheets [85].

3.2.3. Paleoclimatic variability of southern Africa

Comparatively little was known about the paleoclimatic history of southern Africa during this same period, but a recently developed SST record off the coast of Namibia (25°S) documents profound changes over the past 5 Myr. An alkenone-derived SST record and other paleoproductivity indices from ODP Site 1084 [86] demonstrate that the wind-driven Benguela Current upwelling system steadily intensified and SSTs decreased

markedly after 3.2 Ma (Fig. 7), with subsequent sudden periods of intensification (and cooler SSTs) near 2.0 Ma and 0.6 Ma. The greatly di-

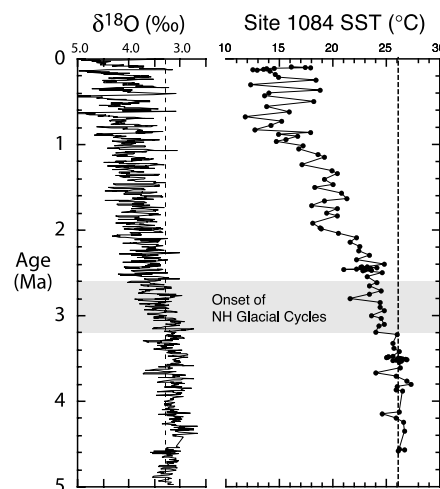


Fig. 7. Marine sediment record of SSTs at South Atlantic ODP Site 1084 (26°S). Alkenone measurements document large (10–15°C) and progressive cooling since 3.2 Ma of the wind-driven Benguela Current upwelling system [86].

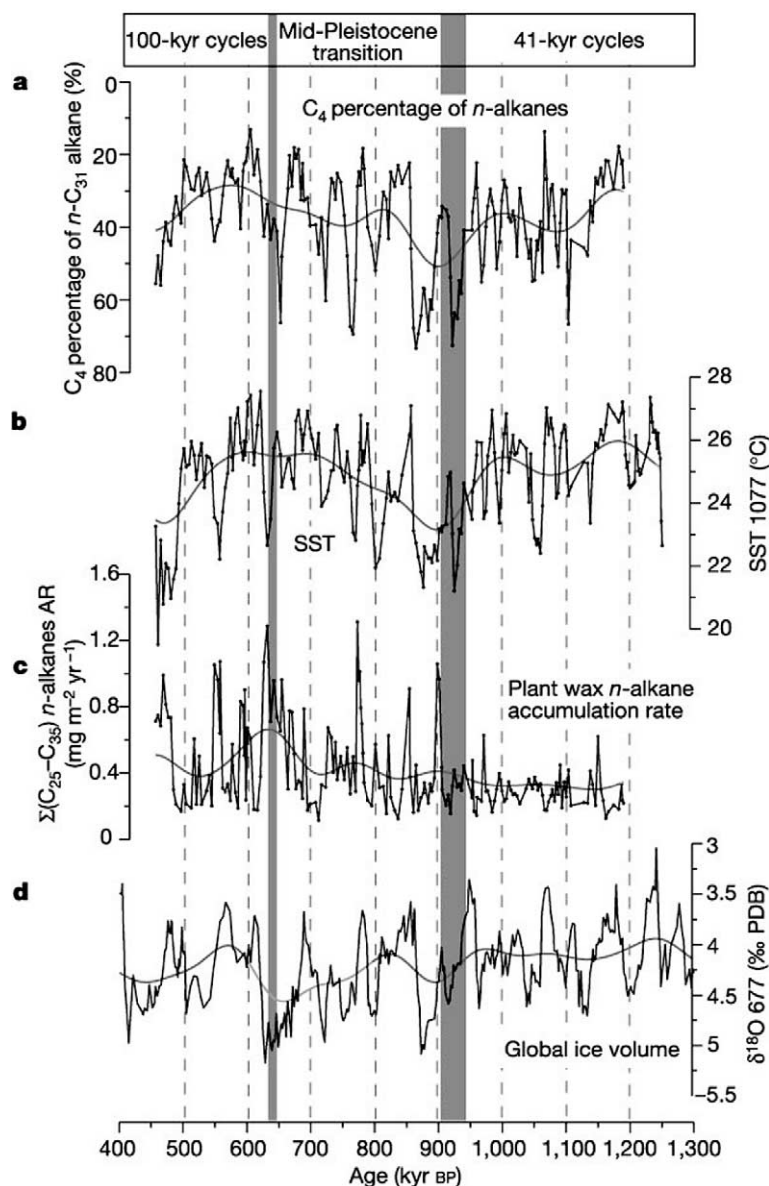


Fig. 8. Middle Pleistocene changes in (a) subtropical South African vegetation, (b) tropical Atlantic SSTs, (c) subtropical South African *n*-alkane fluxes of plant leaf wax compounds, and (d) a benthic oxygen isotopic record of high-latitude ice volume variability. Subtropical South African vegetation changes closely covaried with tropical Atlantic SSTs, and both signals exhibit the same 100 kyr and 41 kyr pacing apparent in high-latitude paleoclimatic records. Increases in arid-adapted (C_4) vegetation are associated with cooler SSTs and glacial maxima [87]. Note the increase in large-amplitude 100 kyr vegetation and SST cycles after ca. 900 ka. Figure reproduced from [87] with permission from *Nature* (Volume 422, pages 418–421) © 2003 Macmillan Publishers Ltd.

minished upwelling and warmer SSTs prior to 3.2 Ma were interpreted to reflect warmer and more stable conditions, with wetter and more mesic environments in southern Africa [86], a conclusion

that is broadly supported by South African paleoecological data [25].

Changes in tropical and south Atlantic SSTs have been shown to be a key determinant regulat-

ing African vegetation changes during the Pleistocene. Schefuss and others [87] used molecular biomarker analyses of plant leaf waxes (*n*-alkanes) preserved in deep-sea sedimentary organic matter at ODP Site 1077 (11°S) to quantify changes in the proportions of arid- (C_4) and humid- (C_3) adapted vegetation in subtropical southwest Africa (Fig. 8). They found that the reconstructed percentage of C_4 vegetation varied between 20 and 70% and that the mid-Pleistocene floral variations were strongly linked to glacial–interglacial variations in tropical SSTs which were also measured at this site using the alkenone method. The records reveal a close correspondence between cooler tropical SSTs and higher percentages of arid-adapted C_4 vegetation during glacial periods (Fig. 8).

3.3. Terrestrial paleoclimatic records

Continuous records of African paleoclimatic change are rare from terrestrial sequences in East Africa because active faulting, erosion, and non-deposition punctuate the geologic record. However, these data provide critical ground truth information on the general Pliocene–Pleistocene development of African climate, as well as specific paleoenvironmental contexts associated with fossil localities. These records generally support the view that East African climate changed from warmer, wetter conditions in the late Miocene and early Pliocene [5,88–90] to a more seasonally contrasted, cooler, and drier and perhaps more variable climate during the late Pliocene (after ca. 3 Ma). Pollen spectra from various fossil sites in NE Africa indicate shifts to cooler and drier vegetation types (increase in shrubs, heath, and grasses) after ca. 2.5 Ma [16]. Stable isotopic analyses of pedogenic carbonates from the Turkana and Olduvai basins indicate gradual replacement of woodland by open savannah grasslands between 3 Ma and 1 Ma, with step-like increases in savannah vegetation near 1.8 Ma, 1.2 Ma and 0.6 Ma [3,4].

The Turkana Basin (Fig. 1a) is one of the best studied depositional basins in East Africa due, in part, to the richness of its fossil record which spans nearly 4.5 Myr. Although it is tempting to

imagine that this basin should have recorded the successions of wet–dry cycles so evident in the marine records, there is little expression of such simple depositional cycles [91,92]. Lake Turkana is presently a closed basin fed by monsoonal runoff from the Ethiopian highlands, but only about 10% of the geologic record there is lacustrine. Still, the Turkana Basin may have recorded some of the climatic oscillations which are evident in deep-sea records. Temporal correlations exist between the Site 721/722 dust record and stratigraphic occurrences of specific moist-indicator lithofacies such as molluscan, ostracod, and other bioclastic sediments in Turkana Basin sequences [93]. There were also several prolonged intervals of continuous lacustrine deposition in the Turkana Basin which persisted for 0.1–0.2 Myr and is represented by interbedded diatomite and claystone deposits. One such lacustrine interval, paleolake Lokochot [93], occurred between 3.4 and 3.5 Ma and is characterized by several decimeter-thick interbeds of diatomite (*Aulacosira* spp.) and clayey siltstone, reflecting oscillations in lake level or sediment supply. Radiometric dates of bounding tephra layers [94] suggest that these bedding cycles were about 20–25 kyr in duration which compares favorably to the precessional cycles evident in the marine paleoclimate records during this time (Fig. 3). Similar bedding cycles for this interval have been noted also in the Middle Awash sequences in Ethiopia [95,96].

4. Pliocene–Pleistocene African faunal evolution

The fossil record of African mammalian evolution suggests important steps in faunal speciation, migration, and adaptation throughout the Pliocene–Pleistocene. In the specific case of early human evolution, behavioral developments are also evident in the archeological record of stone tool use and development. Taphonomic (fossil preservation) and taxonomic (fossil identification) biases can complicate interpretation of faunal trends within and between localities [2], and some localities are additionally impacted by regional tectonic uplift histories which complicate paleoenvironmental interpretations [97,98].

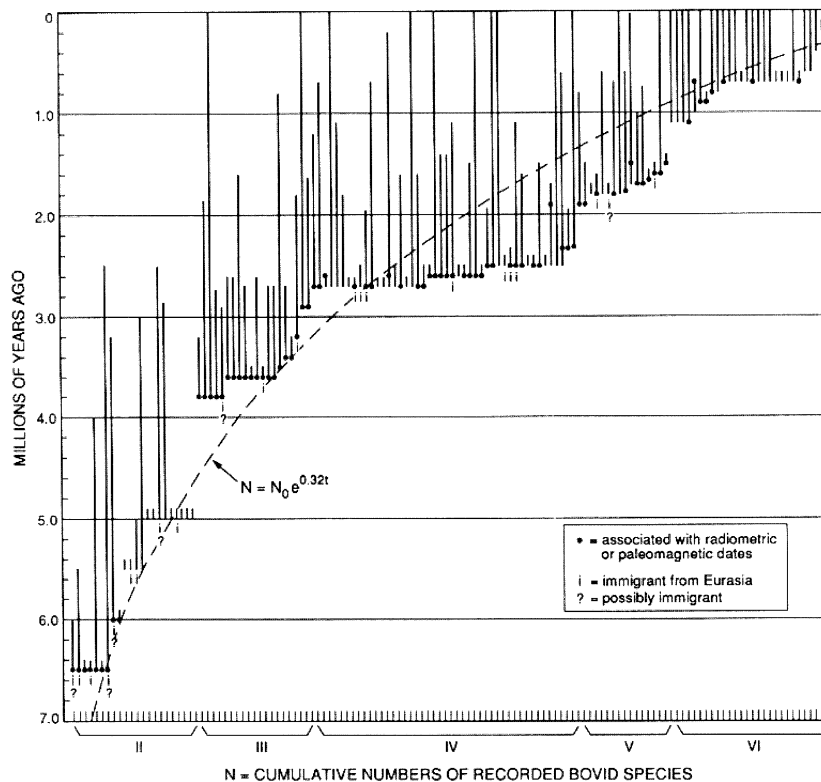


Fig. 9. Range chart of Africa-wide occurrences of fossil bovids (antelope) spanning the last 7 Myr. The dashed line represents a theoretical 'null hypothesis' assuming a uniform rate of faunal turnover (speciation) set at 32% per million years. The pronounced faunal 'turnover pulses', clusters of origination and extinction events, which occurred near 2.8 Ma and 1.8 Ma were also associated with appearances of arid-adapted fauna. A recent reanalysis of a subset of these data, the Omo–Turkana fossil collection, indicates that faunal turnover there was much more gradual and muted [33]. Figure reproduced from [21] with permission from Yale University Press.

4.1. The fossil record of (non-hominid) African mammalian evolution

The fossil record of African bovids (antelope family) is particularly useful for investigating changes in African environments. Bovid fossils typically comprise a large proportion of the total fossil record at any given location, they are highly diverse and represent nearly every environment, and some species are indicative of specific paleoenvironments. Three main approaches have been used to explore the paleoclimatic significance of fossil bovid evolutionary changes: shifts in speciation and extinction rates (turnover) [18,21,28,33,99], shifts in relative abundances of habitat-specific taxa [25,26,32], and changes in the mor-

phology of locomotor limb bones (ecomorphological analyses) [100–102].

An analysis of the entire African bovid fossil record spanning the late Neogene revealed that many first and last appearances of the 127 separate bovid lineages were clustered at 2.7–2.5 Ma, with secondary groupings near ca. 1.8 Ma and ca. 0.7 Ma [21] (Fig. 9). Many of the first appearances near 2.7 Ma were arid-adapted species. In a separate analysis of fossil African micromammal (e.g. rodents) assemblages from the Shungura Formation (Ethiopia), Wessellmann [103] reported a moist-adapted rodent assemblage for Member B (ca. 3 Ma) whereas the fauna in Member F (ca. 2.3 Ma) were dry-adapted.

The turnover pulse hypothesis has been chal-

lenged based on a recent analysis of the Omo–Turkana fossil mammal collection (Fig. 1), one of the richest and best-dated collections in Africa [33]. Calculated faunal turnover in this basin was much less pronounced than in the all-Africa compilation [21], and turnover was found to have occurred more gradually across the 3–2 Ma interval [33]. The absence of a large faunal turnover signal in the Turkana Basin has been attributed to differing analytical protocols, treatment of rare species, and the regional buffering effect of the ancestral Omo River [91]. The evolution of fossil pigs (suids), hominids [34], and carnivores [35] shows similarly little evidence for such focused episodes of faunal turnover. Furthermore, some terrestrial paleoclimatic data indicate that true savannah grasslands were only established after the early and middle Pleistocene [3,4].

Rather than using faunal turnover as the hallmark of environmental change, several recent studies have used the fossil record to examine changes in the abundances of habitat-specific taxa to infer paleoenvironmental shifts. A comprehensive examination of bovid (antelope), cercopithecoid (monkey), and suid (pig) fauna in the Omo sequence in southern Ethiopia [26] (Fig. 1) documented a remarkable decrease in closed woodland and forest species and an increase in grassland species between 3.6 and 2.4 Ma, with a marked rise between 2.6 and 2.4 Ma (Fig. 10). They concluded that “climate change caused significant shifts in vegetation in the Omo paleo-ecosystem” and that “climate forcing in the late Pliocene is more clearly indicated by population shifts within the Omo mammal community than by marked turnover at species level” [26]. This analysis also noted that faunal assemblages became much more variable between adjacent depositional members after 2.6–2.5 Ma. Analysis of East and South African fossil mammal collections also indicates aridification and increased percentages of grazing animals (expanded grasslands), but only after 1.8 Ma [25].

4.2. The fossil record of African hominid evolution

Important Pliocene–Pleistocene events in human evolution post-date the divergence between

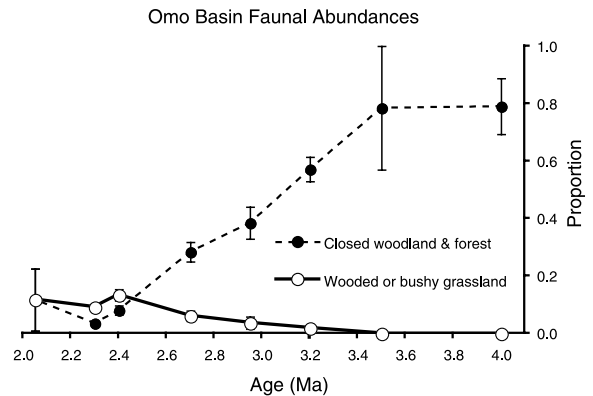


Fig. 10. Relative abundances of two endmember habitat groupings of fossil mammal taxa from the Omo collection during the late Pliocene [26]. Between 3.6 and 2.4 Ma there was a gradual reduction in moist-indicator species corresponding to closed woodland/forest habitats (dashed line), with a significant increase in the proportion of dry-indicator species corresponding to wooded or busy grasslands (solid line) between 2.8 and 2.4 Ma. This study also noted that mammalian faunal assemblages became much more variable between depositional members after 2.6–2.5 Ma, indicating greater long-term ecological instability after this time [2].

ape and human lineages which molecular clock studies estimate to have occurred at about 4.5–6.5 Ma [104–106]. This split is now thought to have occurred significantly earlier based on the recent discovery of *Sahelanthropus tchadensis*, a fossil hominid faunally dated at 6–7 Ma which exhibits both primitive and derived features and is thought to be close to the purported ‘last common ancestor’ [107]. Bipedality is a fundamental characteristic of the human family (Hominidae) and early bipedality is evident in the latest Miocene (ca. 5.8 Ma) hominid *Orrorin tugenensis* [12] and in earliest Pliocene hominid specimens dating to 4.4–4.2 Ma [108–112]. The hominid footprint trackways of three individuals preserved in a volcanic ash bed at Laetoli, northern Tanzania (Fig. 1), provide striking confirmation that obligate bipedality was established by at least 3.6 Ma [13], well before the expansion of savannah grasslands [3].

Fossil hominids are, arguably, the least diagnostic faunal group for investigating past relationships between African climate and faunal change. They are extremely rare (typically less than 1% of a typical assemblage), not particularly useful pa-

leocologically, and they are not very diverse relative to other taxa (only a few different species coexisted at any one time). Still, the Pliocene–Pleistocene fossil record documents fundamental changes in hominid morphology and behavior which can be evaluated within the broader contexts of other faunal and paleoenvironmental changes [1,2,20,23,26,99,113,114].

4.2.1. *Junctures in early human evolution*

Hominid evolution over the Pliocene–Pleistocene interval was punctuated by significant changes in species morphology, innovation, and diversity near 2.8 Ma, 1.7 Ma, and ca. 1 Ma [21,28,114,115]. Radiometric dates constraining most fossils are typically very precise [94,116,117], but the ages of these hominid faunal transitions carry significant uncertainties (± 0.2 Myr) due to gaps in the fossil record, taxonomic uncertainties [118,119], and taphonomic (preservational) biases [114].

The earliest Pliocene hominid species presently documented is the 4.4 Ma *Ardipithecus ramidus* (Fig. 11) based on fragmentary but well-dated fossil evidence from Aramis, Middle Awash in northern Ethiopia [120] (Fig. 1). Dental morphology suggests that *A. ramidus* is the most ‘apelike’ hominid of the ancestral australopithecine lineage. Sedimentological evidence at the site indicates a well-watered wooded habitat in this now hyper-arid terrain [116] which broadly agrees with soil carbonate isotopic evidence for woodland vegetation at many East African fossil localities during the early Pliocene [3,121] (Fig. 11). *Australopithecus anamensis* has been described at several sites near Lake Turkana, Kenya, spanning the interval 4.2–3.9 Ma [122].

Many specimens of *Australopithecus afarensis* (‘Lucy’) have now been described spanning 3.9–2.9 Ma [112,114]. They collectively indicate a single, ecologically diverse, highly sexually dimorphic, bipedal Pliocene hominid whose known range encompassed Ethiopia to Tanzania [112]. Cranial measurements indicate that *A. afarensis* was relatively small-brained, even relative to its body size which was also small relative to subsequent hominid taxa. Analysis of other faunal remains associated with *A. afarensis* specimens from

many regions reveals that members of this taxon were consistently associated with well-watered, wooded paleoenvironments [25].

The recent discovery of a new hominid (*Kenyanthropus platyops*) which was contemporary with *A. afarensis* near 3.5 Ma weakens the case that *A. afarensis* was the root taxon leading to all subsequent hominid taxa [123,124]. *K. platyops* was a particularly important find because it effectively makes the human family tree more complex than previously believed (Fig. 11), and because it possesses characteristics (human-like facial morphology and smaller cheek teeth) which are not seen in the fossil record until the emergence of the first representatives of the *Homo* clade nearly one million years later. A well-watered woodland and woodland mosaic paleoenvironment was indicated from faunal remains at the fossil site (western Turkana Basin, Fig. 1).

4.2.2. *Hominid evolution between 2.9 and 2.4 Ma*

Several fundamental faunal speciation and hominid behavioral changes occur in the fossil record between 2.9 and 2.4 Ma, although the fossil record within this interval is notably poor [114]. At least two new hominid lineages emerged from the ancestral lineage which itself became extinct, and this period marks the first appearance of stone tools (Fig. 11). Earliest members of the ‘robust’ australopithecine genus *Paranthropus* first occur in the fossil record near 2.8 Ma [22,114,125,126]. Among many characteristic anatomical differences, the robustly framed *Paranthropus* were distinguished by uniquely large cheek teeth and strong jaw musculature which apparently reflects a highly specialized masticatory adaptation for processing coarse vegetable matter [23,125,127]. A second lineage, represented by the earliest members of our genus *Homo*, first occurred near 2.3–2.5 Ma [114,115,128] (Fig. 11). Earliest fossils of the *Homo* clade are characterized by a more gracile frame, smaller cheek teeth, and much larger absolute cranial volumes than any prior hominid species [115,118].

The earliest known occurrence of stone tools (the first crude choppers and scrapers comprising the Oldowan complex) is now well dated near 2.3–2.6 Ma [129–133] (Fig. 11). Whether tool

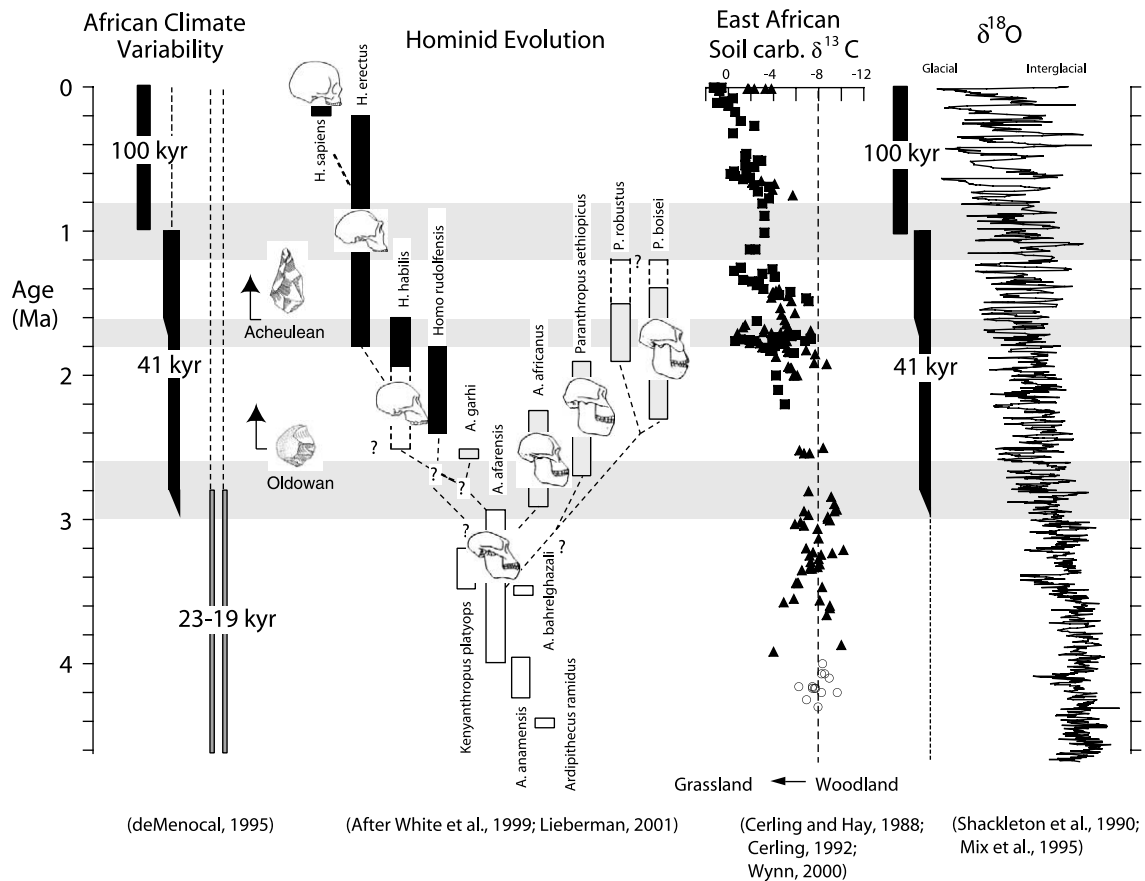


Fig. 11. Summary diagram of important paleoclimatic and hominid evolution events during the Pliocene–Pleistocene. Marine paleoclimatic records indicate that African climate became progressively more arid after step-like shifts near $2.8 (\pm 0.2)$ Ma, and subsequently after $1.7 (\pm 0.1)$ Ma and $1.0 (\pm 0.2)$ Ma, coincident with the onset and intensification of high-latitude glacial cycles [49,50,146]. These events are associated with changes toward dry-adapted African faunal compositions, including important steps in hominid speciation, adaptation, and behavior (see text for discussion). Soil carbonate carbon isotopic data from East African hominid fossil localities document the Pliocene–Pleistocene progressive shifts from closed woodland forest C_3 -pathway vegetation (-9 to -12‰) to arid-adapted C_4 -pathway savannah grassland vegetation ($+2$ to 0‰) (data from Cerling and Hay [4] (solid boxes), Cerling [2] (solid triangles), and Wynn [121] (open circles)).

use was practised exclusively by *Homo* is not known, but the recent discovery of tool cut marks on mammalian bones dated near 2.5 Ma heralds the important behavioral development of meat processing and marrow extraction [130].

The synchronous existence of (at least) two distinct hominid lineages and the emergence of lithic technology has been interpreted to reflect adaptations to a more arid, varied environment [2,22,125]. The 2.9–2.5 Ma interval corresponds

to a period of either modestly [33] or greatly [21] enhanced turnover in fossil bovids (Fig. 9) with associated increases in the proportions of arid-adapted fauna (Fig. 10) [21,26,103]. Analysis of associated faunal remains found with *Paranthropus* fossils from multiple sites indicates they occurred in both wooded and more open paleoenvironments, but always habitats that included wetland fauna [25]. Similar analyses for earliest *Homo* fossils indicate that they were associated

with more varied habitats than any prior hominids [25]. Earliest *Homo erectus* fossils were associated with arid, open grassland environments [25].

4.2.3. Hominid evolution between 1.8 and 1.6 Ma

By 1.8–1.6 Ma, *Homo habilis* became extinct and its immediate successor, and our direct ancestor, *H. erectus*, first occurs in the fossil record near 1.8 Ma [114]. *H. erectus* may have migrated to southeast Asia as early as 1.9–1.8 Ma [134]. Near 1.7 Ma, South African [135] and East African bovid assemblages shift toward further absolute increases in the abundance of arid-adapted species [21] (Fig. 9). Enhanced East African aridity near 1.8–1.6 Ma is supported by soil carbonate stable isotopic evidence for broadly expanded savannah vegetation in East Africa [3,4,136] (Fig. 11). Increased aridity and variability is also evident in the marine paleoclimatic records, particularly those off East Africa (Fig. 2). Earliest occurrences of the more sophisticated Acheulean tool kit (bifacial blades and hand axes) occurred near 1.7–1.6 Ma [132,137] (Fig. 11).

4.2.4. Hominid evolution between 1.2 and 0.8 Ma

The hominid fossil record between 1.4 and 0.8 Ma is notably poor. Available evidence suggests that by 1 Ma the *Paranthropus* lineage had become extinct [114] and *H. erectus* had broadly expanded its geographic range and occupied sites in North Africa, Europe, and western Asia [138,139]. Hominid brain size increased rapidly in later Pleistocene hominid specimens after 780 ka [140,141]. The fossil record of African bovidae suggests a final phase of increased arid-adapted species turnover near 1.2 Ma and 0.6 Ma [21,28,99] (Fig. 9). Soil carbonate isotopic evidence indicates that pure C₄ grasslands, such as the vast savannahs of subtropical Africa today, were only established after ca. 1.2 Ma and after 0.6 Ma [3] (Fig. 11). The marine paleoclimatic records indicate that conditions were not just generally drier but were punctuated by increasingly longer and more severe arid episodes (Figs. 2 and 3). At Olorgesailie (Kenya), successions of fluviolacustrine sediments deposited at about 1.0–0.5 Ma reveal recurrent episodes of large-scale landscape remodeling due to persistent shifts in regional hydrology [2].

5. Summary of major Pliocene–Pleistocene events in African paleoclimatic and faunal change

Taken together, the African faunal and paleoclimatic records suggest three restricted intervals – 2.9–2.4 Ma, 1.8–1.6 Ma, and 1.2–0.8 Ma – when shifts toward increasingly variable, drier African conditions were accompanied by some changes in African faunal assemblages and, perhaps, speciation. Long-term trends toward increased abundances of arid-adapted taxa during the Pliocene–Pleistocene are evident, with indications for faunal changes between 2.9 and 2.4 Ma (the age range encompassing major faunal transitions) and after 1.8 Ma. Challenging many habitat-specific hypotheses, the paleoclimatic record does not support unidirectional shifts to permanently drier conditions. The marine paleoclimate records additionally indicate prolonged (10^4 – 10^5 year) intervals of exceptionally high- and low-amplitude variability, or ‘variability packets’, which may have also presented adaptation pressures [2]. It seems prudent that African climate and faunal evolution hypotheses address the adaptive significance of the higher-frequency (orbital-scale) remodeling of African landscapes [2] as well as the longer-term trends toward more open and more variable environments [2,21].

6. Research frontiers

As evolutionary theorists continue to investigate the possible role of past climate change on African faunal populations there are several promising areas of research which may significantly constrain the problem. These developments include efforts to more thoroughly integrate faunal and paleoclimatic records, and the applications of new analytical tools for reconstructing African vegetation shifts.

Recent years have seen great strides toward more and better integration of African faunal and paleoclimatic datasets. Although well-dated fossil faunal collections have existed for decades in some cases, these datasets have been reanalyzed only very recently for the potential paleoecological content they possess [25,26,100,102]. These

newer studies are distinguished by their application of more sophisticated statistical approaches and classification protocols which have resulted in new records which constrain the timing, amplitude, and ecological contexts of faunal changes during the Pliocene–Pleistocene. The faunal assemblage change evident near 2.8 Ma in the Omo sequence is one such example of the kinds of evidence which may better constrain possible relationships between climate change and evolution [26] (Fig. 10). These studies have benefited from vast improvements in radiometric dating [94,117] and stratigraphic contexts [38,90,92,116,142,143] of fossil material. Dating and correlation of volcanic ash horizons define much of the chronological control for fossil assemblages throughout East Africa [143]. These same ash-fall events are recorded in deep-sea sediment sequences of the Gulf of Aden and Arabian Sea [142,144,145], providing firm stratigraphic ties between the fossil and paleoclimatic records.

The emergence of organic geochemical analytical techniques for isolating and classifying vascular plant leaf wax compounds presents promising opportunities for constraining how and when African vegetation cover changed throughout the Pliocene–Pleistocene. Long-chain, odd-numbered *n*-alkanes are lipid constituents of epicuticular plant leaf waxes which are abraded and transported by winds and are preserved as trace components in the organic fraction of deep-sea sediments [87]. Carbon isotopic analysis of the *n*-alkane fraction is used to quantify the relative proportion of arid-adapted C₄ vegetation sources (e.g. savannah grasses and sedges) [87] (Fig. 8). The application of this method to late Neogene marine sediment sequences off East Africa could settle debates about the timing and nature of African paleoenvironmental shifts and the extent to which these signals impacted African biota.

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