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Astronomically forced climate change in the Kenyan Rift Valley 2.7–2.55 Ma: implications for the evolution of early hominin ecosystems

John D. Kingston^{a,*}, Alan L. Deino^b, Robert K. Edgar^c, Andrew Hill^d

^a Department of Anthropology, Emory University, Atlanta, GA 30322, USA

^b Berkeley Geochronology Center, 2455 Ridge Road, Berkeley, CA 94709, USA

^c Farlow Herbarium of Cryptogamic Botany, Harvard University, Cambridge, MA 02138, USA ^d Department of Anthropology, Yale University, New Haven, CT 06520, USA

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Abstract

Global climate change, linked to astronomical forcing factors, has been implicated in faunal evolutionary change in equatorial Africa, including the origin and diversification of hominin lineages. Empirical terrestrial data demonstrating that orbital forcing has a significant effect, or is detectable, at early hominin sites in equatorial continental interiors during the Pliocene, however, remain limited. Sedimentation patterns in the Baringo Basin within the Central Kenyan Rift Valley between ca. 2.7 and 2.55 Ma, controlled by climatic factors, provide a detailed paleoenvironmental record spanning 35 fossil vertebrate localities, including three hominin sites. The succession includes a sequence of diatomites that record rhythmic cycling of major freshwater lake systems consistent with \sim 23-kyr Milankovitch precessional periodicity. The temporal framework of shifting precipitation patterns, relative to Pliocene insolation curves, implicate African monsoonal climatic control and indicate that climatic fluctuations in Rift Valley ecosystems were paced by global climatic change documented in marine cores. These data provide direct evidence of orbitally mediated environmental change at Pliocene Rift Valley hominin fossil localities, providing a unique opportunity to assess the evolutionary effect of short-term climatic flux on late Pliocene East African terrestrial communities. © 2007 Elsevier Ltd. All rights reserved.

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Introduction

The 3–2 Ma interval represents a threshold period in early hominin evolution. Significant expansion of the cerebral cortex (Tobias, 1995; Holloway, 2000), major cladogenic events resulting in the *Homo* and *Paranthropus* lineages (Walker et al., 1986; Hill et al., 1992; Bromage et al., 1995; Kimbel et al., 1996; Suwa et al., 1996; Harrison, 2002), first manufacture of lithic artifacts (Semaw et al., 2003), and the oldest butchery sites (Asfaw et al., 1999) have all been documented in this interval. Although the specifics of hominin phylogeny

* Corresponding author. *E-mail address:* john.kingston@emory.edu (J.D. Kingston).

are currently debated (e.g., Wood, 1992, 1994, 2002; Suwa et al., 1996; Tattersall and Schwartz, 2000; Wood and Richmond, 2000; White, 2003), the Plio-Pleistocene hominin fossil record of Africa indicates an adaptive radiation of forms, with possibly four australopithecines, three paranthropines, and up to three species of the genus *Homo* occupying the equatorial African landscape during this time, several potentially sympatric. Much research has focused on exploring environmental factors that may be linked to or directly driving these evolutionary transitions (e.g., Brain, 1981; Grine, 1986; Vrba et al., 1989; deMenocal, 1995; Stanley, 1995; Vrba et al., 1995; Bromage and Schrenk, 1999; Bobe et al., in press). During the last decade, views on the environmental context of early hominin evolution have shifted away from interpretations based uniquely on long-term trends or major events towards the notion that in the past local hominin ecosystems fluctuated on short timescales, primarily in response to astronomically-forced global climate change. These oscillations, Milankovitch cycles, result from the interaction of regional climatic systems and shifting patterns of insolation (solar radiation arriving at the top of the Earth's atmosphere), driven by changes in the geometry of the Earth's orbit. The primary orbital cycles invoked include precession (~23 kyr), eccentricity (~100 kyr, 400 kyr), and obliquity (~41 kyr).

Potential links between climate and orbital cycles were recognized (Adhemar, 1842; Croll, 1864) and linked to biotic evolution (Wallace, 1876) as early as the mid-19th century, but a lack of chronologic control hampered attempts to verify any correlations. These ideas were later revived when astronomical signals were experimentally found in geochemical climatic data obtained from a suite of deep-sea cores (Emiliani, 1966; Shackleton, 1967; Hays et al., 1976; Berger, 1977). Data retrieved in these studies revealed the occurrence of numerous, quasi-periodic variations in isotopic parameters with almost constant amplitudes, which could be related directly to orbitally forced climatic cycles using chronometric dating techniques. Since then, periodicities associated with orbital variations have been identified in many paleoclimatic records, and it is clear that orbital forcing is an important factor in climatic fluctuations on the timescale of 10 ka to 1 Ma throughout most of the Earth's history.

Recognizing potential implications for human evolution, a number of researchers suggested that human evolution might be tethered to these quasi-periodic variations logged in marine isotopic records (Brain, 1981; Boaz and Burckle, 1984; Vrba, 1985; Pilbeam, 1989). More recently, specific links between orbitally forced climate change and human evolution have been explored (Potts, 1998; Bonnefille et al., 2004; deMenocal, 2004; Richerson et al., 2005). Empirical evidence of environmental fluctuations at Pliocene hominin localities that can be directly linked to these cycles is limited, however, hampering attempts to develop causal relationships. Pronounced cyclical deposition or evidence of short-term climatic change in the Shungura Formation (Brown, 1969), the Turkana Basin (Brown and Feibel, 1986: Feibel et al., 1989; Brown, 1995; Bobe and Behrensmeyer, 2004; Lepre et al., 2007), at Olduvai Gorge (Hay, 1976; Liutkus et al., 2000; Ashley and Driese, 2003), at Hadar (Bonnefille et al., 2004; Campisano and Feibel, 2007), and Olorgesailie (Potts et al., 1999; Behrensmeyer et al., 2002) have tentatively been linked to orbitally forced climate change. Unequivocal correlation with astronomically mediated insolation patterns remains difficult due to limited chronological control and the confounding effects of tectonic control on sedimentation patterns within Rift Valley settings.

African climate and Milankovitch cycling

Climatic and atmospheric circulation patterns of modern Africa have in general been used to model and interpret conditions during the Pliocene with the assumption that these patterns have remained generally consistent over the last 5 Ma. Equatorial African climate is currently controlled by the intersection of three major convergence zones, superimposed on and influenced by regional factors associated with rift-related topography, coastal currents and upwelling, and sea surface temperature fluctuations in the Indian and Atlantic Oceans (Nicholson, 1996, 2000). As a result, climatic patterns are markedly complex and highly variable. Latitudinal position and seasonal migration of the Intertropical Convergence Zone exert a significant influence on precipitation patterns, resulting in a general bimodal seasonal distribution of rainfall in equatorial regions with maxima occurring in the two transitional seasons (April-May and October-November). Solar radiation is significant in sustaining tropical convergence, and studies of shifts in equatorial African paleoenvironments and paleoclimate have implicated orbitally forced changes in insolation . Although obliquity, eccentricity, and precession signals have all been identified in paleoclimatic proxies, Pliocene and Pleistocene circulation in the tropics appears to have been paced primarily by precessional variation in insolation (Pokras and Mix, 1985, 1987; Bloemendal and deMenocal, 1989; Molfino and McIntyre, 1990; Tiedemann et al., 1994). Strong eccentricity and obliquity amplitude signals have also been identified (deMenocal, 1995; Lourens et al., 1996; D'Argenio et al., 1998; Moreno et al., 2001; Gorgas and Wilkens, 2002; Jahn et al., 2003). The coexistence of all main Milankovitch cycles in spectra data may provide evidence for a complex interdependence and influence of high- and low-latitude orbital parameters influencing climatic regimes in equatorial Africa. El Nino-Southern Oscillation linked fluctuations in precipitation (Verschuren et al., 2000a), threshold effects resulting in abrupt transitions (deMenocal et al., 2000; Thompson et al., 2002), provisional correlations with Heinrich events and Dansgaard-Oeschger cycles (Stager et al., 2002), and linear and nonlinear Earth-intrinsic feedback mechanisms of the climatic system (Kutzbach et al., 1996; Gorgas and Wilkens, 2002) further complicate simple interpretations of external forcing of tropical African paleoclimates.

Tugen Hills geology and paleontology

The Tugen Hills is a complex fault block uplifted along a synthetic fault (Saimo Fault) between the Elgeyo Escarpment and the axial Baringo-Suguta trench within the central Kenyan Rift (Fig. 1a). The rift in this area was initiated as a down-warped trough in the early to middle Miocene and has served as a depositional basin for thick and widespread sedimentary sequences over the past 16 Ma (Chapman et al., 1978; King, 1978). Subsequent structural deformation, uplift, and erosion have exposed extensive Miocene and Pliocene fossiliferous strata over an area of > 2,400 km² along the eastern foothills, the crest of the Tugen Hills, and to the west of the Tugen Hills in the Kerio Valley (Figs. 1b, 2). Sediments within the succession have yielded abundant and diverse faunal assemblages (Bishop et al., 1971; Bishop and Pickford, 1975;



Fig. 1. (a) Location map of the Tugen Hills and Baringo Basin within the Central Kenyan Rift Valley. (b) Map depicting distribution of exposed Chemeron Formation sediments along the eastern flanks of the Tugen Hills, just west of Lake Baringo.

Pickford, 1975a,b, 1978a,b; Hill, 1985; Hill et al., 1985; Hill, 1995), including a number of hominid and hominin specimens (Pickford, 1978b; Pickford et al., 1983; Hill, 1985, 1994; Hill and Ward, 1988; Hill et al., 1992, 2002; Ward et al., 1999; Senut et al., 2001; Sherwood et al., 2002a, 2002b). Much research has also focused on documenting the paleoecology throughout the succession through analyses of fossil floral (Jacobs and Kabuye, 1987, 1989; Jacobs and Winkler, 1992; Jacobs and Deino, 1996; Jacobs, 1999; Kingston et al., 2002) and biogeochemical proxies (Kingston et al., 1994; Morgan et al., 1994; Kingston, 1999). These data are unique in providing a framework in which hominin evolutionary and environmental change can be assessed locally through the late Neogene without the need to create a long-term ecological composite based on evidence gathered from geographically distant sites.

Data from the Tugen Hills have revealed a complex evolutionary history of ecosystems characterized by spatial and temporal heterogeneity with no clear evidence of any long-term trends. While these studies suggest that the patterns of heterogeneity may be shifting at short timescales $(10^4 - 10^5 \text{ kyr})$, limited temporal resolution has until now precluded assessments of environmental change at these scales.

Chemeron Formation

Within the succession, the Chemeron Formation encompasses a series of discontinuous exposures of Pliocene and Pleistocene sediments and tuffs along the eastern foothills of the Tugen Hills (Fig. 1b). Strata in the formation span approximately 3.7 million years, from about 5.3 Ma at the base to 1.6 Ma near the top (Fig. 2; Deino and Hill, 2002; Deino et al.,



Fig. 2. Generalized composite stratigraphic framework of the Tugen Hills Succession, depicting the interval of Chemeron Formation analyzed in this study.

2002). Sedimentary and tuffaceous rocks of the Chemeron Formation, formally designated by McCall et al. (1967), were deposited disconformably on the Kaparaina Basalts and are overlain unconformably by the middle Pleistocene Kapthurin Formation (Pickford, 1975a, 1975b; Chapman et al., 1978; Pickford et al., 1983; Hill et al., 1986; Williams and Chapman, 1986). At least two distinct Chemeron depositional basins have been recognized (Martyn, 1967, 1969; Chapman et al., 1978; Hill, 1985) and there has been considerable debate on the nomenclature of sediments to be included or excluded from the Chemeron Formation (Chapman, 1971; Pickford, 1975b; Chapman et al., 1978; Hill et al., 1986). In general, two areas of major outcrop have been identified: the Chemeron Basin in the south, currently dissected by the modern Chemeron, Ndau, Barsemoi, and Kapthurin Rivers, and the Kipcherere Basin 10 km to the northwest (Figs. 1b, 3; Martyn, 1967). Isolated exposures of Chemeron sediments, correlated laterally utilizing distinctive tuff units and stratigraphically underlying Kaparaina lavas (Pickford, 1975b; Deino et al., 2002), extend a further 15-20 km to the north of the Kipcherere Basin along the zone of the Saimo Escarpment.

Chemeron strata in the younger southeastern depositional basin typically range from less than 3.2 Ma to about 1.6 Ma (Hill et al., 1992; Deino and Hill, 2002). These sediments either disconformably overlie or are in fault contact with basaltic lavas and minor intercalated sediments of the 5.7–5.1 Ma Kaparaina Basalt (Chapman and Brook, 1978; Hill, 1985; Deino et al., 2002). The uppermost Chemeron



Fig. 3. Geologic map of Chemeron Formation exposed in the Barsemoi, Ndau, and Kapthurin Rivers and associated drainages, comprising the core study area within the southern Chemeron Depositional Basin. Depicted are locations of vertebrate fossil localities and stratigraphic sections shown in Fig. 4. See Fig. 1b for map location.

Formation consists of 3-5 m of sediments that overlie the 1.57 Ma Ndau Trachymugearite mafic flow (Chapman and Brook, 1978; Hill et al., 1986).

Chemeron paleolakes

Within the southern depositional basin, Chemeron sediments are exposed as an eastward-dipping structural block (~20–30°), highly disrupted by ~north-south (N-S) normal faults (Fig. 3). This sequence consists primarily of terrigineous and lacustrine sediments-primarily mudstone, siltstone, and sandstone with intercalations of tuff, diatomite, and conglomerate. Within this general succession, a distinctive lithologic package characterized by a series of diatomite units and interbedded fluvial and alluvial fan detritus and tuffs can be traced > 5-6 km N-S along strike (Figs. 1b, 3, 4). Diatomites, $\sim 3-7$ m thick, consist exclusively of freshwater lacustrine diatom frustules and document significant, intermittent lake systems within the axial portion of the rift. Thickness of specific diatomite units is highly variable between sections, indicating irregular lake bathymetry, differential deposition due to bottom currents, or variable diatom production. While there is no consistent N-S trend in diatomite thickness variability, multiple repetition of the section by N-S normal faults provides an east-west (E-W) dimension for sequence, revealing a slight eastward thickening



Fig. 4. Stratigraphic sections of portions of the Chemeron Formation between ca. 3.0-2.4 Ma. Location and lateral correlation of diatomite horizons, tuff horizons, 40 Ar/ 39 Ar dated tuff horizons (units), and fossil localities are indicated. Depicted timescale relates specifically to regressed sedimentation rates based on 40 Ar/ 39 Ar tuff dates derived directly from, or correlated directly to, stratigraphic section A–A'(Deino et al., 2006). Unit ages represent weighted-mean ages of individual sample ages derived from the same tuff horizon. Stratigraphic thickness of diatomites, and especially interbedded terrigineous sediments, varies considerably reflecting large-scale lateral facies variation.

trend. This may reflect sediment focusing (Lehman, 1975; Hilton, 1985), suggesting that deeper portions of the paleolakes were located towards the axes of the rift. Ongoing reconnaissance of Chemeron Formation exposures south of the Ndau River and north of the Kapthurin River has so far failed to reveal margins of the paleolakes.

Regression/transgression considerations

Assuming that the western paleolake margins were controlled by the north-south tectonic rift fabric, the current north-south orientation of diatomite exposures roughly parallel paleoshorelines. As such, these exposures essentially represent a single point on the regression-transgression continuum as lake levels shift in response to climatic control. The Barsemoi diatomites represent primarily deep lake facies as lake levels rose rapidly, inundating an extensive portion of the Baringo Basin. In this respect, alternation of aquatic and subaerial facies in the Barsemoi sequence depict shifting lake levels at a specific elevation and do not necessarily indicate a lack of paleolakes in deeper or more axial portions of the rift lake(s) during non-diatomite deposition locally.

Depositional transitions between the diatomites and stratigraphically adjacent fluvial and alluvial fan sediments are characterized by relatively abrupt transgressive and regressive sequences. Diatomites are typically bracketed by 20–30 cm fine sand and silt horizons containing fish fossils, which grade into high-energy terrestrial facies indicating relatively rapid cycling between deep lake and fully subaerial conditions. The rarity of littoral diatoms within these transitions (see below) also indicates rapid shifts in lake levels.

Extent of paleolakes

A variety of features of the Barsemoi diatomites indicates that they are the products of large paleolakes, which were probably moderately deep (>30-40 m), areally significant (at least several hundred km^2), and stable (ca. 5–10 kyr) features of the Pliocene landscape, with central basins isolated from fringing littoral zones and terrigineous input. The diatomites are purely diatomaceous (sensu Owen, 2002), being composed almost entirely (>90% by volume) of the intact and fragmented siliceous cell walls of planktonic species of two diatom genera, Aulacoseira and Stephanodiscus (Fig. 5). Within the five diatomites, there is no hiatus in diatom deposition and no significant dilution of the diatoms by fluviatile clastic detritus. A lack of mixing with terrigeneous input suggests that deposition of the Barsemoi diatomites was on the order of at least 5 km from a shoreline based on modern East African lake analogs (Owen and Crossley, 1992). Quantitative examination of samples from Chemeron Formation diatomite strata (n = 488) indicate than >90% of all diatoms in each sample, at virtually all levels in each diatomite unit, are euplanktonic species of the genera Aulacoseira [e.g., A. granulata (Ehr.) Simonsen; A. agassizi (Ostenf.) Simonsen] and Stephanodiscus [e.g., S. cf. astrea (Ehr.) Grun.; S. cf. hantzschii Grun.; S. cf. subtransylvanicus Gasse]. These species are also part of the present-day and Holocene diatom record of large lakes from which paleoenvironmental inferences are



Fig. 5. Diatomites 3 and 4, bracketed by subaerial sediments, exposed in the main Barsemoi river channel. A.H. for scale. Diatomites are comprised almost exclusively of the genera *Stephanodiscus* and *Aulacoseira*.

derived. Samples with a similar high dominance of these combined genera characterize the present-day phytoplankton and sediments of some of the large lakes of the Western and Southern Rift Valley, such as Lake Malawi, Tanganyika, and Rukwa (Talling, 1986; Haberyan and Hecky, 1987; Hecky and Kling, 1987; Pilskahn and Johnson, 1991; Owen and Crossley, 1992; Gasse et al., 2002), the late Pleistocene-Holocene diatom record of these large lakes (Haberyan, 1987; Haberyan and Hecky, 1987; Owen and Crossley, 1992), and that of Lake Victoria (Stager, 1984; Stager et al., 1997), and the diatomites resulting from the large Ethiopian Pliocene Lake Gadeb (Gasse, 1980). The samples display a marked rarity of periphytic and facultatively planktonic diatoms (Gasse, 1980) derived from littoral regions. The relative abundance of littoral diatoms, which are produced in the sunlit shallows of a lake, is characteristically < 5% in samples from these diatomites, with a mode of 1-2%. This low fraction is characteristic of offshore plankton samples from southern Lake Malawi (Haberyan and Mhone, 1991) and is markedly low compared to the 10-80% littoral diatoms characteristic of the present-day Holocene sediments of the shallow Lakes Naivasha (Verschuren et al., 2000a; Trauth et al., 2003) and Magadi (Barker et al., 1990) and the shallower regions or low-stand stages of large lakes (Gasse, 1980; Haberyan, 1987; Gasse and van Campo, 1998; Telford and Lamb, 1999). The diatom flora of the shallow aquatic ecosystems, such as ponds, swamps, and springs of the Borgoria-Baringo region of Kenya (Owen et al., 2004), has virtually no taxonomic similarity to the Barsemoi diatomites. [Planktonic/(periphytic + facultative planktonic)] ratios of > 100 generally indicate deep lakes (Trauth et al., 2005). Using this criterion, the Barsemoi paleolake depths would be on the order of > 150 m. Shallow lakes during periods of sustained low precipitation and high evaporation, which are common in East African climatic history, or of mineral-laden groundwater input, can evolve to become 'soda' or saline lakes, which are characteristic of the present-day and Holocene lakes in the Eastern Rift Valley. Under such ecological conditions, saline or hypersaline diatoms are strongly represented in the sediments (Haberyan, 1987; Barker et al., 1990; Telford and Lamb, 1999; Verschuren et al., 2000a,b). No such highly alkaline or saline flora has been observed in the Barsemoi diatomites. Lastly, in examining about 10% of the total samples (selected either randomly or based on an exfoliation when immersed in water), a majority of these exhibited light microscopic evidence of intact Aulacoseira filaments of 5-10 cells and, in some, an apparent segregation of Aulacoseira and Stephanodiscus into fine laminae, indicating an anoxic hypolimnion in the lakes in which these diatomaceous sediments were formed (Pilskahn and Johnson, 1991; Pilskahn, 2004). Lake stratification, by limiting the depth of turbulent mixing and anoxia and preventing the feeding and burrowing by in-sediment animals, dampens those processes primarily responsible for the fragmentation of Aulacoseira filaments and homogenization of their benthic temporal layering. Fossil records of such diatom laminae have been reported primarily from large lakes (Haberyan and Hecky, 1987; Owen and Crossley, 1992; Owen and Utha-aroon, 1999). East African lakes, except for the very largest ones, seasonally mix to about 20–40 m (Baxter et al., 1965; Haberyan, 1987; Hecky and Kling, 1987), or to their bottoms if they are shallower, suggesting that the Barsemoi paleolakes were at least this deep.

Intra- and inter diatomite variability

There is substantial and significant nonrandom variation in the relative abundances of Aulacoseira and Stephanodiscus at 10-cm intervals within and among diatomites (Fig. 6). The relative abundance of Aulacoseira ranges from $\approx 0\%$ to 100%, whereas *Stephanodiscus* ranges from 0% to \approx 100%. The temporal and spatial abundances of the species of these two genera present in East African lakes and Pliocene-Recent deposits are thought to be causally determined primarily by their resource requirements for silicon and phosphorus (as an Si:P ratio) and light (Kilham, 1971; Tilman et al., 1982; Gasse et al., 1983; Kilham et al., 1986; Kilham, 1990). Aulacoseira requires a relatively high Si:P and is adapted to low light conditions. In contrast, Stephanodiscus is a successful competitor when Si:P is low, but requires both high phosphorus and high light levels. The distribution of these nutrients with respect to light is largely under the control of a lake's hydrodynamics (Talling, 1986; Haberyan and Hecky, 1987; Kilham, 1990; Gasse et al., 2002; Owen, 2002). When lakes mix deeply, especially to or near their bottoms, Aulacoseira predominates. However, when lakes thermally stratify, restricting the depth of mixing, the euphotic zone is more conducive to the growth of Stephanodiscus. The mixing regime is largely determined by the intensity of upwelling, by the wind's intensity, duration, and direction (fetch), and by the heat balance of the lake as reflected in its temperature, its thermal stratification gradients, and its conductive, convective, and radiative interactions with the atmosphere (Lehman et al., 1998; Lehman, 2002). Thus, the present interpretation of Aulacoseira (A)-Stephanodiscus (S) variation rests on the causal connections among changes in mixing regimes and specific nutrient resource distributions. Ultimately, these factors are controlled by climate (Owen and Crossley, 1992; Stager et al., 2002, 2003), with the proportion of *Stephanodiscus* [S/(A+S)] varying directly with atmospheric temperature and inversely with windiness. Aulacoseira predominates under cool windy conditions; Stephanodiscus under warmer, less windy conditions (Gasse et al., 2002).

The pattern of diatom distribution indicates a maximum relative abundance of *Stephanodiscus* in diatomites 2 and 3, the minima in bracketing diatomites 1 and 5 (Fig. 6). Differences in the proportions of *Stephanodiscus* among adjacent diatomites are statistically significant (Kolmogorov-Smirnov and Mann Whitney p < 0.001 for all pairs, except between diatomites 2 and 3, where p < 0.05). Median [S/(A + S)] ratios range from 0.11 and 0.07 for the earliest and latest diatomites to 0.69, 0.57, and 0.31 for diatomites 2, 3, and 4, respectively. These data indicate a cycling trend within the 2.58–2.7 Ma interval of maximum amplitude of insolation resulting from eccentricity modulation of precessional shifts during this interval



Fig. 6. The distribution of the relative abundance of *Stephanodiscus* across the five diatomites as shown by 388 samples taken at 10-cm intervals within each diatomite. No macroscopic layering of the diatomites was evident in the field, so samples were chosen based on position along the 'vertical' transect alone, where a roughly $1 \times 2 \times 2$ cm³ block of diatomite was collected. The 1 cm dimension more-or-less paralleled the line of transect. Examination of each block was based on an approximately $3 \times 3 \times 3$ mm³ subsample, dispersed vigorously in distilled water and then strewn on a coverglass and mounted in [®]Hyrax for a light microscope (LM) census of taxa. The proportion of *Stephanodiscus* [= S/(A + S)] is based on a valve count of *Stephanodiscus* (S) plus *Aulacoseira* (A), which was effectively the sum of all diatoms counted in a sample. The sample size for each proportion was 100–500 valves, with the size being sufficient to provide a 95% confidence interval for each proportion estimate of \pm 0.05, with the exception of the basal sample in diatomite 5, where the interval is probably twice as large. *Stephanodiscus* dominance is interpreted as indicating less windy and warmer climatic conditions; *Aulacoseira* dominance windier and cooler conditions. Box and Whisker plots based on collective data from each of the diatomites, indicating the median, interquartile range, and overall range of data. Preliminary stable carbon isotopic analyses of organic matrix, sequestered within the diatom biosilica, is shown for diatomites 2 and 3. The data suggest ¹³C enrichment upsection within these two horizons, possibly linked to changes in the A/(A + S) ratio related to climatic conditions.

(Fig. 7d, see discussion below). The maximum insolation values associated with each of the diatomites are similar (520, 520, 519, 520, and 525 W/m² for diatomites 1–5, respectively) suggesting that this cycling is not simply a function of shifting insolation values and perhaps involves threshold effects or involvement of regional or global climatic response to orbital forcing. These cycles documented in the Barsemoi diatomites result in hydrological changes stemming from changes in the precipitation and evaporation balance in the Baringo Basin and in the hydrographical mixing dynamics in its paleolakes. Overall, proportions of *Stephanodiscus* indicate an increase in temperature and less windy conditions as the diatomites develop in the sequence and then a return to original conditions by the last diatomite.

Relative proportions of the two dominant genera of diatoms also vary considerably and significantly within each of the Barsemoi diatomites. Diatom samples at 10-cm intervals reflect timescales on the order of 10^3 years, and it remains unclear as to whether these fluctuations occur at this scale or shorter time intervals. In some of the samples, the apparent segregation of Aulacoseira and Stephanodiscus into subtle layers on a scale of $<100 \,\mu\text{m}$ and the presence of microlaminae on a scale of one hundred to a few hundred microns suggest cyclic variation in a time frame of one to a few years. These laminae are reminiscent of seasonal couplets and annual to multiannual cycles for these taxa, or processes affecting their abundance, reported in Holocene and recent East African lakes (Habervan, 1987; Habervan and Hecky, 1987; Pilskahn and Johnson, 1991; Owen and Crossley, 1992; Pilskahn, 2004). Cumulatively, these observations indicate that although the large Barsemoi paleolakes persisted for thousands of years in response to intensified monsoonal systems, each of the diatomites exhibits evidence of lower-order cycling.

Links between paleolakes and orbitally forced climatic change

A high-resolution chronostratigraphic framework has been developed for the sequence based on series of ⁴⁰Ar/³⁹Ar ages analyses from eight primary, anorthoclasebearing tephra units from stratigraphic sections measured in the Barsemoi Tributary and adjacent drainages (Fig. 4; Hill et al., 1992; Deino et al., 2002, 2006). Tuffs were dated in replicate from samples collected in parallel sections. The local stratigraphic sequence ranges from 3.1-2.35 Ma with five diatomites confined to the 2.69-2.58 Ma interval. Based on ⁴⁰Ar/³⁹Ar ages of intercalated tuffs, a uniform sediment accumulation rate (16 cm/kyr) was calculated for the sequence and used to interpolate the ages for the upper and lower contacts of each of the five diatomites (Deino et al., 2006). These data indicate that the median time interval between the onset of the diatomite sedimentation cycles is 23.2 kyr (range 22-27 kyr) and 23.4 kyr between their termination (range 22–27 kyr), suggesting that the lake cycling is controlled or heavily influenced by precessional insolation forcing. For the precessional parameter, the most important terms in the series expansion of the equation correspond to periods of 23,700 years and 22,400 years; the next three terms are close to 19,000 years.

Intercalibration of the astronomical timescale with carefully determined ⁴⁰Ar/³⁹Ar ages (Kuiper, 2003; Kuiper et al., 2004; Deino et al., 2006) provides a means of orbitally tuning the Barsemoi sequence. Uncertainties in the astronomical polarity timescale (APTS) adjusted diatomite ages are on the order of $\pm 0.3\%$ (or ± 8 kyr) sufficiently precise to tune the Barsemoi sequence uniquely to the APTS. In addition, identification of the Gauss/Matuyama paleomagnetic polarity transition in the Barsemoi within the upper part of one of the diatomites (Fig. 4.) independently leads to the same tuning by reference to this boundary's position in open-ocean marine cores (Lisiecki and Raymo, 2005; Deino et al., 2006). This makes it possible to directly compare the age of the Barsemoi paleolakes with a series of theoretically calculated insolation curves and potentially identify specific climatic components controlling lake levels in the Rift Valley during the middle Pliocene. Humidity/aridity cycles in equatorial Africa have been linked to changes in insolation at various latitudes and cycle frequencies. Available data have been variously interpreted to support three general models of control of low-latitude African aridity patterns and direct the selection of appropriate insolation curves to consider for correlation with the Barsemoi diatomites (Fig. 7h-j.).

One model implicates insolation forcing of the African monsoon via heating of North Africa and resulting land-sea pressure contrasts (Kutzbach, 1981). Increasing insolation at approximately 30°N during boreal summer intensifies the southwest African monsoon and the penetration of moist air masses into equatorial Africa from the Atlantic Ocean (Fig. 7h). These cycles occur primarily at the 23-kyr tempo of Earth-orbital precession. Monsoonal control is supported by records of shifting Quaternary lake levels in North Africa (Street-Perrott and Harrison, 1984; Kutzbach and Street-Perrott, 1985; Pokras and Mix, 1985, 1987; Gasse et al., 1989; Lamb et al., 1995) and by formation of sapropelitic muds in the Eastern Mediterranean Basin. Formation of these sapropels is linked to high freshwater and organic discharge from the Nile, whose headwaters drain East African highlands, therefore reflecting northern East African precipitation patterns (Rossignol-Strick et al., 1982; Rossignol-Strick, 1983).

More recently, a second model has been proposed based on investigations in the Naivasha Basin, Central Kenyan Rift Valley. These studies suggest that seasonal rains in East Africa are in part triggered by increased March or September insolation on the equator at half-precession cycles. High insolation intensifies the intertropical convergence and convective rainfall in the region (Fig. 7i,j; 2003). These patterns also operate at 23-kyr precessional frequencies. This model also challenges the notion that the terrestrial tropics play a passive role in global climate linkages, instead suggesting that the terrestrial tropics and surrounding oceans may generate higher-latitude changes (Leuschner and Sirocko, 2003; Trauth et al., 2003; Barker et al., 2004).



A third model advocates that sub-Saharan moisture patterns are linked to northern latitude glacial/interglacial cycling at eccentricity and obliquity amplitudes or timing (Fig. 7f,g). Evidence for this view includes regional eolian and biogenic dust transport patterns (deMenocal, 1995; Moreno et al., 2001), upwelling patterns adjacent or near the African coast (Gorgas and Wilkens, 2002), biochemical and biotic bedding patterns in coastal sediments (D'Argenio et al., 1998), and rhythmic stratification patterns in subtropical African lakes (Scholz, 2000; Ficken et al., 2002; Johnson et al., 2002).

Cycles of increased lake levels in Baringo 2.7-2.5 Ma, as recorded by diatomites, are most consistent with the first model, implicating intensification of the monsoonal system as the main control on precipitation patterns during this interval in the Baringo Basin. Absolute ages of the diatomites relative to calculated ETP (eccentricity/tilt/precession) insolation curves most closely correspond to insolation maxima at 30°N in June/July (Fig. 7h; Deino et al., 2006). Although cycling of the Barsemoi diatomites is precessionally driven at 23-kyr intervals, this series of paleolakes coincides with a period of high insolation linked to high eccentricity modulation of insolation between $\sim 2.5-2.8$ Ma. These data suggest a threshold effect, whereby formation and persistence of deep perennial lake systems within the axial rift are contingent on achieving and maintaining a minimum level of low-latitude insolation above which the monsoonal system provides sufficient precipitation for the formation of rift lakes.

Under- and overlying Chemeron strata within the sequence. correlating to lower insolation maxima, are essentially devoid of diatomites or other significant lacustrine facies. Temporally adjacent envelopes of maximum eccentricity modulated precession at ~2.9-3.1 Ma and ~2.1-2.35 Ma did not apparently result in the development of a series of significant lake systems in this portion of the rift, despite greater relative insolation amplitude for these flanking intervals (Fig. 7a,b,d). A single diatomite at ~ 3.1 Ma in the Barsemoi section hints at higher lake levels during the earlier maximum insolation envelope (Fig. 7h). Unlike the younger diatomites, the age of this paleolake or lake high-stand is imprecisely known as it is based on an extended extrapolation of sedimentation rates. Control of lake formation in this portion of the rift may typically be dominated by tectonic processes, with the Barsemoi diatomites representing a window of tectonic quiescence or stability during which pervasive climatic patterns could be recorded. Alternatively, isolated development of paleolake systems in the Baringo Basin 2.7-2.55 Ma may reflect a unique combination of interactions between global climate boundary conditions and shifts in the African monsoon intensity related to orbital forcing. The Barsemoi paleolakes coincide with the onset and intensification of the Northern Hemisphere Glaciation at ~ 2.75 Ma. This event marks one of the critical climate thresholds in the Cenozoic, marked by a progressive ¹⁸O enrichment in benthic foraminifera between 3.1 and 2.5 Ma and the massive appearance of ice-rafted debris in northern high-latitude oceans (Shackleton et al., 1984). Analyses of marine records of eolian dust contributions indicate a dominance shift from 23-kyr precessional periodicity to 41-kyr obliquity variance at about this time as well, suggesting that the African climate became more arid and sensitive to high-latitude climatic forcing (deMenocal and Bloemendal, 1995; Maslin et al., 1998; Trauth et al., 2005). Comparison of Barsemoi paleolake cycling with the orbitally tuned climate proxy dust record from ODP site 721/722 in the Arabian Sea (deMenocal and Bloemendal, 1995) indicates synchronicity at the precessional phase in the two climatic records. The timing of Barsemoi diatomites correlates with terrigineous input minima into the Arabian Sea, which are interpreted to reflect more humid conditions in subtropical Africa (Fig. 7e). Within the Barsemoi succession, it remains difficult to evaluate the effects of obliquity or the relative dominance of obliquity or precession in controlling East African precipitation patterns during this time.

Ecological response of Rift Valley ecosystems

Having documented significant orbitally forced climate change within the Rift Valley, how do organisms respond to these oscillations and what, if any, are the evolutionary consequences? Milankovitch cycles operate at timescales much greater than the generation times of mammals but significantly shorter than most species durations [~ 2.5 Ma (Stanley, 1985; Alroy, 2000)]. The overall frequency of evolutionary response to precessional cycling is so low that evolutionary stasis dominates the adaptive landscape for most species at this scale. In addition, the resolution of the Pliocene terrestrial fossil record is currently far too coarse to detect or assess biological

Fig. 7. (a–d) Temporal range of the Barsemoi diatomite package and general range of local Chemeron Formation sediments situated within shifting patterns of calculated astronomical parameters (INSOLA program:Laskar et al., 2004) spanning the last 3.5 Ma. Proposed humid phases are based on known lacustrine sequences documented in the East African Rift Valley (Trauth et al., 2005). Approximate timing of three major global climatic transitions are also indicated as in Trauth et al. (2005)—intensification of Northern Hemisphere Glaciation (Haug and Tiedemann, 1998), intensification and shifting of the Walker Circulation (Ravelo et al., 2004), and initiation of the Mid-Pleistocene Revolution (Berger and Jansen, 1994). (e–j) Absolute ages of Barsemoi diatomite horizons (depicted as vertical shaded bands) juxtaposed against: e) ODP 721/722 eolian dust curves (deMenocal and Bloemendal, 1995); f–g) calculated obliquity and eccentricity curves (Paillard et al., 1996; http://www.agu.org/eos_elec/96097e.html); and h–j) relevant insolation curves (Laskar et al., 2004) for the 2.35–3.1 Ma interval. Lake high-stands, characterized by diatomite occurrence, correlate most closely with insolation curves for 30°N during June/July (h), indicating intensified precipitation maxima corresponding to an intensified low-level monsoonal flow. Pleistocene sedimentary records at Lake Naivasha (120 km south of the Baringo Basin in the Rift Valley) indicate lake high-stands follow maximum equatorial solar radiation in March and September, supporting the concept of a direct relation-ship between increased insolation heating and an intensification of the intertropical convergence and convective rainfall over East Africa (Trauth et al., 2003; i and j). There is no obvious correlation between we tintervals in the Baringo Basin as reflected by diatomites ordicate dated allowenceal and Bloemendal, 1995). Oldest Barsemoi diatomite (at ca. 3.06 Ma) is depicted as a dashed line to indicate that the age of the lake represented is not as precisely const

response at a timescale of $10^4 - 10^5$ yrs. It has been suggested that changes in the amplitude and periodicity of orbitally forced climatic variability may have contributed to faunal turnovers (Vrba, 1995; Dynesius and Jansson, 2000; deMenocal, 2004). Late Neogene turnover cycles in micromammal lineages in Spain have been correlated with low-frequency modulation of Milankovitch oscillations (2.4–2.5 and 1.0 Myr), implicating astronomical climate forcing as a major determinant in rodent lineage turnover (van Dam et al., 2006).

Within the local Barsemoi sequence, 35 vertebrate fossil localities have been documented and ten sites have so far been tied directly into the stratigraphic sections exhibiting cycling (Figs. 3, 4). Preliminary assessments of mammalian faunal communities in the sequence indicate that there are no macroevolutionary shifts that can be specifically linked with lake cycling and that major lineages are continuous through the diatomaceous interval where significant environmental fluctuation is evident.

Three sites have yielded hominin fragments, including a temporal bone attributed to Homo sp. indet. at 2.43 Ma (Hill et al., 1992; Deino and Hill, 2002; Sherwood et al., 2002b), a molar fragment with affinities to Paranthropus at ca. 2.9 Ma, and a premolar fragment identified as Hominini gen. et sp. indet. (but distinct from Homo) also at ca. 2.9 Ma (Fig. 4). As with most of the vertebrate fossil material, the hominins are associated with terrestrial horizons bracketing lacustrine deposits, and it is currently difficult to assess any specific shifts in faunal communities that might be associated with 'wet' and 'arid' phases. Fossils of colobines and Theropithecus-typically interpreted as forest and open woodland/ grassland primates, respectively-have been recovered from isochronous horizons at several localities throughout the sequence, suggesting habitat heterogeneity. Representative taxa of suids, rhinoceratids, hippos, bovids, and giraffids have consistently been identified at scattered Chemeron horizons through the 2.8-2.4 Ma interval, indicating lineage persistence and relative long-term community stability despite environmental flux. Ongoing studies are examining vertebrate faunal distribution in the succession.

While it may not be appropriate or possible to link macroevolutionary change with short-term Milankovitch cycling, orbitally forced climatic oscillations have significant effects on biota that cumulatively may pace speciation and extinction events. Precession modulated cycling of precipitation and seasonality patterns in the Rift Valley during the Pliocene and Pleistocene presumably resulted in dynamic fluctuations in the physiognomy and taxonomic representation of flora in the region, with more arid and seasonal climatic regimes generally associated with more widespread open woodland and grassland habitats. The immediate response of vegetation to this short-term climatic variability would likely have involved a reshuffling of the relative coverage of different plant communities rather than whole-scale extinction or speciation events. Studies of Quaternary paleovegetation records indicate that equatorial African ecosystems are highly sensitive to orbitally forced climate change, associated atmospheric CO₂ shifts, and vegetation-soil feedbacks, resulting in rapid shifts

in pollen assemblage indices (Lézine, 1991; Bonnefille and Mohammed, 1994; Elenga et al., 1994, 2004), charcoal-fluxes (Verardo and Ruddiman, 1996), and relative proportions of C_3 (trees, shrubs, cold-season grasses and sedges) and C_4 (warmseason grasses and sedges) biomarkers (Huang et al., 1999; Ficken et al., 2002; Schefuß et al., 2003). These studies also indicate that vegetation is responding to environmental change at scales significantly shorter than precessional cycles, probably related to the complex interaction of the many factors controlling precipitation, temperature, and seasonality patterns.

Specific response of Rift Valley plant paleocommunities to precessional cycling of Barsemoi paleolake systems is difficult to predict or model, primarily as the configuration of climatic parameters responsible for the hydrological cycling remain unknown. The simplest interpretation would be to assume that high lake levels, correlated to maximum insolation at 30°N latitude, reflect increasing total annual precipitation resulting from intensification of African monsoonal systems. These conditions would be associated with more wooded or forested ecosystems. Climatic controls on lake levels, however, are contingent on overall precipitation/evaporation regimes, which in turn are based on seasonal distribution of rainfall and temperature ranges. Lake transgressions may be due to cooler temperatures and decreased evaporation at key intervals in annual or biannual seasonal patterns of rainfall rather than strictly to increased precipitation.

The primary response of terrestrial fauna to these oscillations would likely be through changes in the size and location of species' geographic distribution (Bennett, 1997). Rather than directing the relocation of entire communities, environmental change more likely causes species to respond individualistically, to migrate in different directions and at different times, and reassemble in new species associations, resulting in repeated fragmentation and rearrangement of communities (Graham, 1986; Huntley and Webb, 1989; Bennett, 1990). Dispersal of species into novel, variable environments and communities can cumulatively lead to microevolutionary change in isolated populations and ultimately increase the potential for speciation or extinction events (Barnosky, 2005).

In addition to habitat tracking, various adaptive strategies have been proposed as options for terrestrial taxa faced with environmental instability including phenotypic plasticity, developmental plasticity, or behavioral flexibility (Bennett, 1997; Dynesius and Jansson, 2000; Jansson and Dynesius, 2002; Barnosky and Bell, 2003). It has been argued that recurrent and rapid climatic oscillations favor speciation resulting in higher taxonomic diversity and phenotypic disparity (Valentine, 1984; Vrba, 1992; Moritz et al., 2000). Shifting periodicities can affect the duration of phases during which species' geographic distributions remain continuously fragmented and organisms must exist beyond vicariance thresholds (outside optimal range), increasing the incidence of speciation and extinction (Vrba, 1995). Others have suggested that orbitally forced climatic shifts generally increase gene flow directly by reshuffling gene pools, and that any microevolutionary change that accumulates on a timescale of thousands of years

is consequently lost as communities reorganize following climate change (Bennett, 1990). Oscillations indirectly select for vagility (dispersal ability and propensity) and generalism that can reduce extinction in the long run and also slow speciation rates (Dynesius and Jansson, 2000; Jansson and Dynesius, 2002). According to the variability selection hypothesis (Potts, 1996, 1998), complex intersection of orbitally forced changes in insolation and Earth-intrinsic feedback mechanisms results in extreme, inconsistent environmental variability selecting for behavioral and morphological mechanisms that enhance adaptive variability. Assessing the relative validity of these evolutionary models ultimately hinges on developing a level of temporal and spatial resolution in the faunal record to anchor micro- and macroevoltuionary events in the context of short-term environment shifts. This also requires documenting and assessing the relative magnitude and significance of environmental variability occurring at various orbital and submillenial scales.

Conclusions

Rift-related ecosystems of East Africa are unique in tropical Africa in their topographically mediated habitat heterogeneity, localized climatic patterns, and perennial lake systems. While early stages of human evolution were not confined to Rift Valley ecosystems, early hominins utilized these distinctive biomes. Reconstructing environmental flux in these habitats has significance for interpreting selective pressures faced by our ancestral populations. Climatically controlled shifts in paleohydrological patterns in the Baringo Basin evident between 2.5 and 2.7 Ma represent a window on a much more pervasive pattern of environmental change that is generally obscured locally and regionally by rifting activity. Dramatic oscillations in lake levels in the Baringo Basin, as indicated by the cycling of diatomites, occur at 23-kyr intervals that can be linked to precessional insolation. The timing of the paleolakes most closely approximates insolation maximum for the June/July 30°N insolation curve, suggesting that precipitation patterns in the region were controlled by the African monsoon system in the middle Pliocene. Significant taxonomic variation in diatoms within each of the diatomites imply lower-order cycling, some reminiscent of seasonal couplets and annual to multiannual cycles. The Baringo data reinforce the perspective that hominin evolution in the Rift Valley, and in tropical Africa in general, should be evaluated more in the context of shifting patterns of precessional-scale and lower-order environmental flux rather than long-term $(>10^{5})$ trends. Climatic and geological instability combined with habitat heterogeneity result in highly dynamic selective forces on early hominins and their communities. These oscillations cause repeated fragmentation and alteration of early hominin communities, resulting in the dispersal of populations to highly variable regional ecosystems and potential peripatric or allopatric speciation events. The challenge remains to identify and link specific shifts in ecological paleocommunities, intraspecific diversity, phenotypic variability, and biogeographic patterns in early hominin evolution at the temporal scale of shifting patterns of precessionally forced and submillennial climatic change.

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References

- Adhemar, J.A., 1842. Revolutions de la mer, Deluges Periodics, Carillian-Goeury et V. Dalmont, Paris.
- Alroy, J., 2000. New methods for quantifying macroevolutionary patterns and processes. Paleobiology 26, 707–733.
- Asfaw, B., White, T., Lovejoy, O., Latimer, B., Simpson, S., Suwa, G., 1999. *Australopithecus garh*: a new species of early hominid from Ethiopia. Science 284, 629–635.
- Ashley, G.M., Driese, S.G., 2003. Paleopedology and paleohydrology of a volcaniclastic paleosol interval; implications for early Pleistocene stratigraphy and paleoclimate record, Olduvai Gorge, Tanzania. J. Sed. Res. 70, 1065–1080.
- Barker, P., Gasse, F., Roberts, N., Taieb, M., 1990. Taphonomy and diagenesis in diatom assemblages: a Late Pleistocene palaeoecological study from Lake Magadi, Kenya. Hydrobiologia 214, 267–272.
- Barker, P.A., Talbot, M.R., Street-Perrott, R.A., Marret, R., Scourse, J., Odada, E.O., 2004. Late Quaternary climatic variability in intertropical Africa. In: Battarbe, R.W., Gasse, F., Stickley, C.E. (Eds.), Past Climate Variability through Europe and Africa. Springer, Dordrecht, pp. 117–138.
- Barnosky, A.D., 2005. Effects of Quaternary climatic change on speciation in mammals. J. Mammal. Evol. 12, 247–264.
- Barnosky, A.D., Bell, C.J., 2003. Evolution, climatic change and species boundaries: perspectives from tracing *Lemmiscus surtatus* populations through time and space. Proc. Royal Soc. Lond. B 270, 2585–2590.
- Baxter, R.M., Prosser, M.V., Talling, J.F., Wood, R.B., 1965. Stratification in tropical, African lakes of moderate altitudes. Limnol. Oceanogr. 10, 510–520.
- Behrensmeyer, A.K., Potts, R., Deino, A., Ditchfield, P., 2002. Olorgesailie, Kenya: A million years in the life of a rift basin. In: Renault, R.W., Ashley, G.M. (Eds.), Sedimentation in Continental Rifts. SEPM Spec. Pub., no. 73, pp. 97–106.
- Bennett, K.D., 1990. Milankovitch cycles and their effects on species in ecological and evolutionary time. Paleobiology 16, 11–21.
- Bennett, K.D., 1997. Evolution and Ecology: The Pace of Life. Cambridge University Press, Cambridge. 241.
- Berger, A., 1977. Support for the astronomical theory of climatic change. Nature 269, 44–45.

- Berger, W.H., Jansen, E., 1994. Mid-Pleistocene Climate Shift The Nansen connection. In: Johannessen, O.M., Muench, R.D., Overland, J.E. (Eds.), The Polar Oceans and Their Role in Shaping the Global Environment. Am. Geophys. Union Geophys. Monogr. 85, 295–311.
- Bishop, W.W., Pickford, M., 1975. Geology, fauna and paleoenvironment of the Ngorora Formation, Kenya Rift Valley. Nature 254, 185–192.
- Bishop, W.W., Chapman, G.R., Hill, A., Miller, J.A., 1971. Succession of Cainozoic vertebrate assemblages from the northern Kenya Rift Valley. Nature 233, 389–394.
- Bloemendal, J., deMenocal, P., 1989. Evidence for a change in the periodicity of tropical climate cycles at 2.4 Myr from whole-core magnetic susceptibility measurements. Nature 342, 897–899.
- Boaz, N.T., Burckle, L.H., 1984. Paleoclimatic framework for African hominid evolution. In: Vogel, J.C. (Ed.), Late Cainozoic Palaeoclimates of the Southern Hemisphere. Balkema, Rotterdam, pp. 483–490.
- Bobe, R., Behrensmeyer, A.K., 2004. The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. Palaeogeogr. Palaeoclim. Palaeoecol. 207, 399–420.
- Bobe, R., Alemseged, Z., Behrensmeyer, A.K. (Eds.). Hominin environments in the East African Pliocene: an assessment of the faunal evidence. Vertebrate Paleobiology and Paleoanthropology Series, vol. 1. Springer, Dordrecht, in press.
- Bonnefille, R., Mohammed, U., 1994. Pollen-inferred climatic fluctuations in Ethiopia during the last 3,000 years. Palaeogeogr. Palaeoclim. Palaeoecol. 109, 331–343.
- Bonnefille, R., Potts, R., Chalie, F., Jolly, D., Peyron, O., 2004. High-resolution vegetation and climate change associated with Pliocene Australopithecus afarensis. Proc. Natl. Acad. Sci. 101, 12125–12129.
- Brain, C.K., 1981. The evolution of man in Africa: was it a consequence of Cainozoic cooling? Alex L. du Toit Mem. Lecture 17. Trans. Geol. Soc. S. Afr. Annex 84, 1–19.
- Bromage, T.G., Schrenk, F. (Eds.), 1999. African Biogeography, Climate Change, and Human Evolution. Oxford University Press, New York.
- Bromage, T.G., Schrenk, F., Zonneveld, F., 1995. Paleoanthropology of the Malawi-Rift: an early hominid mandible from the Chiwondo Beds, northern Malawi. J. Hum. Evol. 28, 71–108.
- Brown, F.H., 1969. Observations on the stratigraphy and radiometric age of the Omo Beds, southern Ethiopia. Quaternaria 11, 7–14.
- Brown, F.H., 1995. The Turkana Basin and Paleoclimatic Reconstruction in East Africa. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven, pp. 319–330.
- Brown, F.H., Feibel, C.S., 1986. Revision of the lithostratigraphic nomenclature in the Koobi Fora region, Kenya. J. Geol. Soc. Lond. 143, 297–310.
- Campisano, C.J., Feibel, C.S., 2007. Connecting local environmental sequences to gobal climate patterns: evidence from the hominin-bearing Hadar Formation, Ethiopia. J. Hum. Evol. 53, 515–527.
- Chapman, G.R., 1971. The geological evolution of the northern Kamasia Hills, Baringo District, Kenya. Ph.D. Thesis, University of London.
- Chapman, G.R., Brook, M., 1978. Chronostratigraphy of the Baringo Basin, Kenya. In: Bishop, W.W. (Ed.), Geological background to fossil man. Scottish Academic Press, London, pp. 207–223.
- Chapman, G.R., Lippard, S.J., Martyn, J.E., 1978. The stratigraphy and structure of the Kamasia Range, Kenya Rift Valley. J. Geol. Soc. Lond. 135, 265–281.
- Croll, J., 1864. On the physical cause of the change of climate during geological epochs. Philosophical Magazine 28, 121–137.
- D'Argenio, B., Fischer, A.G., Richter, G.M., Longo, G., Pelosi, N., Molisso, F., Morais, M.L.D., 1998. Orbital cyclicity in the Eocene of Angola: visual and image-time-series analysis compared. Earth Planet. Sci. Lett. 160, 147–161.
- Deino, A.L., Hill, A., 2002. ⁴⁰Ar/³⁹Ar dating of Chemeron Formation strata encompassing the site of hominid KNM-BC 1, Tugen Hills, Kenya. J. Hum. Evol. 42, 141–151.
- Deino, A.L., Kingston, J.D., Glen, J.M., Edgar, R.K., Hill, A., 2006. Precessional forcing of lacustrine sedimentation in the late Cenozoic Chemeron Basin, Central Kenya Rift, and calibration of the Gauss/Matuyama boundary. Earth Planet. Sci. Lett. 247, 41–60.

- Deino, A.L., Tauxe, L., Monaghan, M., Hill, A., 2002. ⁴⁰Ar/³⁹Ar geochronology and paleomagnetic stratigraphy of the Lukeino and lower Chemeron Formations at Tabarin and Kapcheberek, Tugen Hills, Kenya. J. Hum. Evol. 42, 117–140.
- deMenocal, P.B., 1995. Plio-Pleistocene African climate and the paleoenvironment of human evolution. Science 270, 53–59.
- deMenocal, P.B., 2004. African climate change and faunal evolution during the Pliocene-Pleistocene. Earth Planet. Sci. Lett. 220, 3–24.
- deMenocal, P.B., Bloemendal, J., 1995. Plio-Pleistocene climatic variability in subtropical Africa and the paleoenvrionment of hominid evolution. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven, pp. 262–288.
- deMenocal, P., Ortiz, J., Guilderson, T., Adkins, J., Sarnthein, M., Baker, L., Yarusinsky, M., 2000. Abrupt onset and termination of the African Humid Period: rapid climate responses to gradual insolation forcing. Quatern. Sci. Rev. 19, 347–361.
- Dynesius, M., Jansson, R., 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. Proc. Natl. Acad. Sci. 97, 9115–9120.
- Elenga, H., Maley, J., Vincens, A., Farrera, I., 2004. Palaeoenvironments, palaeoclimates and landscape development in Atlantic Equatorial Africa: A review of key sites covering the last 25 kyrs. In: Battarbe, R.W., Gasse, F., Stickley, C.E. (Eds.), Past Climate Variability through Europe and Africa. Springer, Dordrecht, pp. 181–198.
- Elenga, H., Schwartz, D., Vincens, A., 1994. Pollen evidence of late Quaternary vegetation and inferred climate changes in Congo. Palaeogeogr. Palaeoclim. Palaeoecol. 109, 345–356.
- Emiliani, C., 1966. Paleotemperature analysis of Caribbean cores P6304-8 and P6304-9 and a generalized temperature curve for the past 425,000 years. J. Geol. 74, 109–126.
- Feibel, C.S., Brown, F.H., McDougall, I., 1989. Stratigraphic context of fossil hominids from the Omo Group deposits: northern Turkana Basin, Kenya and Ethiopia. Am. J. Phys. Anthropol. 78, 595–622.
- Ficken, K.J., Woodler, M.J., Swain, D.L., Street-Perrott, F.A., Eglinton, G., 2002. Reconstruction of a subalpine grass-dominated ecosystem, Lake Rutundu, Mount Kenya: a novel. Palaeogeogr. Palaeoclim. Palaeoecol. 177, 137–149.
- Gasse, F., 1980. Les Diatomées lacustres Plio-Pléistocenes du Gadeb (Éthiopie): Systématique, paléoécologie, biostratigraphie. Revue Algologique Mémoire 3.
- Gasse, F., Barker, P., Johnson, T.C., 2002. A 24,000 yr diatom record from the northern basin of Lake Malawi. In: Odada, E., Olago, D.O. (Eds.), The East African Great Lakes: Limnology, Paleolimnology and Biodiversity. Kluwer, Dordrecht, Netherlands, pp. 393–414.
- Gasse, F., Ledee, V., Massault, M., Fontes, J.-C., 1989. Water-level fluctuations of Lake Tanganyika in phase with oceanic changes during the last glaciation and deglaciation. Nature 342, 57–59.
- Gasse, F., Talling, D.F., Kilham, P., 1983. Diatom assemblages in East Africa: classification, distribution and ecology. Révue d'Hydrobiologie Tropicale 16, 3–34.
- Gasse, F., van Campo, E., 1998. A 40,000-yr pollen and diatom record from Lake Tritrivakely, Madagascar, in the southern tropics. Quatern. Res. 49, 299–311.
- Gorgas, T.J., Wilkens, R.H., 2002. Sedimentation rates off SW Africa since the late Miocene deciphered from spectral analyses of borehole and GRA bulk density profiles: ODP sites 1081–1084. Marine Geol. 180, 29–47.
- Graham, R.W., 1986. Response of mammalian communities to environmental changes during the late Quaternary. In: Diamond, J., Case, T.J. (Eds.), Community Ecology. Harper and Row, New York, pp. 300–313.
- Grine, F.E., 1986. Ecological causality and the pattern of Plio-Pleistocene hominid evolution in Africa. S. Afr. J. Sci. 82, 87–89.
- Haberyan, K.A., 1987. Fossil diatoms and the paleolimnology of Lake Rukwa, Tanzania. Freshwater Biol. 17, 429–436.
- Haberyan, K.A., Hecky, R.E., 1987. The late Pleistocene and Holocene stratrigraphy and paleolimnology of Lakes Kivu and Tanganyika. Palaeogeogr. Palaeoclim. Palaeoecol. 61, 169–197.

- Haberyan, K.A., Mhone, O.K., 1991. Algal communites near Cape Maclear Southern Lake Malawi Africa. Hydrobiologia 215, 175–188.
- Harrison, T., 2002. The first record of fossil hominins from the Ndolanya Beds, Laetoli, Tanzania. Am. J. Phys. Anthropol. 119, 83.
- Haug, G.H., Tiedemann, R., 1998. Effect of the formation of the Isthmus of Panama on Atlantic Ocean thermohaline circulation. Nature 393, 673–676.
- Hay, R.L., 1976. Geology of the Olduvai Gorge. University of California Press, Berkeley.
- Hays, J.D., Imbrie, J., Shackleton, N.J., 1976. Variations in the earth's orbit: pacemaker of the ice ages. Science 194, 1121–1132.
- Hecky, R.E., Kling, H.J., 1987. Phytoplankton ecology of the great lakes of the rift valleys of Central Africa. Archiv für Hydrobiologie Beheifte Ergebnisse Limnologie 25, 197–228.
- Hill, A., 1985. Early hominid from Baringo, Kenya. Nature 315, 222-224.
- Hill, A., 1994. Late Miocene and Early Pliocene hominoids from Africa. In: Corruccini, R.S., Ciochon, R.L. (Eds.), Integrative paths to the past. Prentice Hall, Englewood Cliffs, New Jersey, pp. 123–145.
- Hill, A., 1995. Faunal and environmental change in the Neogene of East Africa: Evidence from the Tugen Hills Sequence, Baringo District, Kenya. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven, pp. 178–193.
- Hill, A., Curtis, G., Drake, R., 1986. Sedimentary stratigraphy of the Tugen Hills. In: Frostick, L.E., Renaut, R.W., Reid, I., Tiercelin, J.J. (Eds.), Sedimentation in the African Rifts. Geol. Soc. London, Spec. Pub., No. 25, pp. 285–295.
- Hill, A., Drake, R., Tauxe, L., Monaghan, M., Barry, J.C., Behrensmeyer, A.K., Curtis, G., Jacobs, B.F., 1985. Neogene palaeontology and geochronology of the Baringo Basin, Kenya. J. Hum. Evol. 14, 759–773.
- Hill, A., Leakey, M., Kingston, J.D., Ward, S., 2002. New cercopithecoids and a hominoid from 12.5 Ma in the Tugen Hills succession, Kenya. J. Hum. Evol. 42, 75–93.
- Hill, A., Ward, S., 1988. Origin of the Hominidae: the record of African large hominoid evolution between 14 and 4 my. Yearb. Phys. Anthropol. 31, 49-83.
- Hill, A., Ward, S., Deino, A., Garniss, C., Drake, R., 1992. Earliest *Homo*. Nature 355, 719–722.
- Hilton, J., 1985. A conceptual framework for predicting the occurrence of sediment focusing and sediment redistribution in small lakes. Limnol. Oceanogr. 31, 1169–1181.
- Holloway, R.L., 2000. Brain. In: Delson, E., Tattersall, I., Couvering, J.V., Brooks, A.S. (Eds.), Encyclopedia of Human Evolution and Prehistory. Garland Publishing, Inc., New York, pp. 141–149.
- Huang, Y., Street-Perrott, F.A., Perrott, R.A., Metzger, P., Eglinton, G., 1999. Glacial-Interglacial environmental changes inferred from molecular and compound-specific d¹³C analyses of sediments from Sacred Lake, Mt. Kenya. Geochim. Cosmochim. Acta 63, 1383–1404.
- Huntley, B., Webb, T., 1989. Migration: species' response to climatic variations caused by changes in the Earth's orbit. J. Biogeogr. 16, 5–19.
- Jacobs, B.F., 1999. Estimation of rainfall variables from leaf characters in tropical Africa. Palaeogeogr. Palaeoclim. Palaeoecol. 145, 231–250.
- Jacobs, B.F., Deino, A.L., 1996. Test of climate-leaf physiognomy regression models, their application to two Miocene floras from Kenya, and ⁴⁰Ar/³⁹Ar dating of the Late Miocene Kapturo site. Palaeogeogr. Palaeoclim. Palaeoecol. 123, 259–271.
- Jacobs, B.F., Kabuye, C.H.S., 1987. A middle Miocene (12.2 Ma) forest in the East African Rift Valley, Kenya. J. Hum. Evol. 6, 147–155.
- Jacobs, B.F., Kabuye, C.H.S., 1989. An extinct species of *Pollia* (Commelinaceae) from the Miocene Ngorora Formation, Kenya. Rev. Palaeobot. Palynol. 59, 67–76.
- Jacobs, B.F., Winkler, D.A., 1992. Taphonomy of a middle Miocene autochthonous forest assemblage, Ngorora Formation, central Kenya. Palaeogeogr. Palaeoclim. Palaeoecol. 99, 31–40.
- Jahn, B., Donner, B., Muller, P.J., Rohl, U., Schneider, R.R., Wefer, G., 2003. Pleistocene variations in dust input and marine productivity in the northern Benguela Current: evidence of evolution of global glacial-interglacial cycles. Palaeogeogr. Palaeoclim. Palaeoecol. 193, 515–533.

- Jansson, R., Dynesius, M., 2002. The fate of clades in a world of recurrent climate change: Milankovitch oscillations and evolution. Ann. Rev. Ecol. Syst. 33, 741–777.
- Johnson, T.C., Brown, E.T., McManus, J., Barry, S., Barker, P., Gasse, F., 2002. A high-resolution paleoclimate record spanning the past 25,000 years in southern East Africa. Science 296, 113–132.
- Kilham, P., 1971. A hypothesis concerning silica and the freshwater planktonic diatoms. Limnol. Oceanogr. 16, 10–18.
- Kilham, P., 1990. Ecology of *Melosira* species in the Great Lakes of Africa. In: Tilzer, M.M., Serruya, C. (Eds.), Large Lakes: Ecological Structure and Function. Springer-Verlag, Berlin, pp. 414–427.
- Kilham, P., Kilham, S.S., Hecky, R.E., 1986. Hypothesized resource relationships among African planktonic diatoms. Limnol. Oceanogr. 31, 1169–1181.
- Kimbel, W.H., Walter, R.C., Johanson, D.C., Reed, K.E., Aronson, J.L., Assefa, Z., Eck, G.G., Bobe, R., Hovers, E., Rak, Y., York, D., Chen, Y., Evensen, N.M., Smith, P.E., 1996. Late Pliocene Homo and Oldowan tools from the Hadar Formation (Kada Hadar Member), Ethiopia. J. Hum. Evol. 31, 549–561.
- King, B.C., 1978. Structural and volcanic evolution of the Gregory Rift Valley. In: Bishop, W.W. (Ed.), Geological Background to Fossil Man. Scottish Academic Press, London, pp. 29–54.
- Kingston, J.D., 1999. Environmental determinants in early hominid evolution: issues and evidence from the Tugen Hills, Kenya. In: Andrews, P., Banham, P. (Eds.), Late Cenozoic Environments and Hominid Evolution: A Tribute to Bill Bishop. Geological Society, London, pp. 69–84.
- Kingston, J.D., Jacobs, B.F., Hill, A., Deino, A., 2002. Stratigraphy, age and environments of the late Miocene Mpesida Beds, Tugen Hills, Kenya. J. Hum. Evol. 42, 95–116.
- Kingston, J.D., Marino, B.D., Hill, A., 1994. Isotopic evidence for Neogene hominid paleoenvironments in the Kenya Rift Valley. Science 264, 955–959.
- Kuiper, K., 2003. Direct intercalibration of radio-isotopic and astronomical time in the Mediterranean Neogene. Geologica Ultraiectina 235, 147–165.
- Kuiper, K.F., Hilgen, F.J., Steenbrink, J., Wijbrans, J.R., 2004. Ar⁻⁴⁰/Ar⁻³⁹ ages of tephras intercalated in astronomically tuned Neogene sedimentary sequences in the eastern Mediterranean. Earth Planet. Sci. Lett. 222, 583–597.
- Kutzbach, J.E., 1981. Monsoon climate of the Early Holocene: climate experiment with the Earth's orbital parameters for 9,000 years ago. Science 214, 59–61.
- Kutzbach, J.E., Bonan, G., Foley, J., Harrison, S.P., 1996. Vegetation and soil feedbacks on the response of the African monsoon to orbital forcing in the early to middle Holocene. Nature 384, 623–626.
- Kutzbach, J.E., Street-Perrott, F.A., 1985. Milankovitch forcing of fluctuations in the level of tropical lakes from 18 to 0 kyr BP. Nature 317, 130–134.
- Lamb, H., Gasse, G., Benkaddour, A., Hamoutl, N.E., Kaars, S.B.D., Perkins, W.T., Pearce, N.J., Roberts, C.N., 1995. Relationship between century-scale Holocene arid intervals in tropical and temperate zones. Nature 373, 134–137.
- Laskar, J., Robutel, P., Joutel, F., Gastineau, M., Correia, A.C.M., Levrard, B., 2004. A long-term numerical solution for the insolation quantities of the Earth. Astron. Astrophys. 428, 261–285.
- Lehman, J.T., 1975. Reconstructing the rate of accumulation of lake sediment: the effect of sediment focusing. Quatern. Res. 5, 541–550.
- Lehman, J.T., 2002. Application of satellite AVHRR to water balance and mixing dynamics and the chemistry of Lake Edward, East Africa. In: Odada, E.O., Olaga, D.O. (Eds.), The East African Great Lakes: Limnology, Paleolimnology and Biodiversity. Kluwer, Dordrecht, pp. 235–260.
- Lehman, J.T., Muggide, R., Lehman, D.A., 1998. Lake Victoria plankton ecology: mixing depth and climate-driven control of lake condition. In: Lehman, J.T. (Ed.), Environmental Change and Response in East African Lakes. Kluwer, Dordrecht, pp. 99–116.
- Lepre, C.J., Quinn, R.L., Joordens, J.C.A., Swisher, C.C., Feibel, C.S., 2007. Plio-Pleistocene facies environments from the KBS Member, Koobi Fora Formation: implications for climate controls on the development of lakemargin hominin habitats in the northeast Turkana Basin (northwest Kenya). J. Hum. Evol. 53, 504–514.
- Leuschner, D.C., Sirocko, F., 2003. Orbital insolation forcing of the Indian Monsoon—a motor for global climate changes. Palaeogeogr. Palaeoclim. Palaeoecol. 197, 83–95.

- Lézine, A.-M., 1991. West African paleoclimates during the last climatic cycle inferred from an Atlantic deep-sea pollen record. Quartern. Res. 35, 456–463.
- Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic d¹⁸O records. Paleoceanography 20, PA1003.
- Liutkus, C.M., Ashley, G.M., Wright, J.D., 2000. Short-term changes and Milankovitch cyclicity at Olduvai Gorge, Tanzania; evidence from sedimentology and stable isotopes. Abstracts with Programs — GSA 32, 21.
- Lourens, L.J., Antonarakou, A., Hilgen, F.J., Van Hoof, A.A.M., Vergnaud-Grazzini, C., Zachariasse, W.J., 1996. Evaluation of the Plio-Pleistocene astronomical timescale. Paleoceanography 11 (4), 391–413.
- Martyn, J., 1967. Pleistocene deposits and new fossil localities in Kenya. Nature 215, 476–480.
- Martyn, J.E., 1969. The geological history of the country between Lake Baringo and the Kerio River, Baringo District, Kenya. Ph.D. Thesis, University of London.
- Maslin, M.A., Li, X.S., Loutre, M.F., Berger, A., 1998. The contribution of orbital forcing to the progressive intensification of northern hemisphere glaciation. Quatern. Sci. Rev. 17, 411–426.
- McCall, G.J.H., Baker, B.H., Walsh, J., 1967. Late Tertiary and Quaternary sediments of the Kenya Rift Valley. In: Bishop, W.W., Clark, J.D. (Eds.), Background to Evolution in Africa. Chicago University, Chicago, pp. 191–220.
- Molfino, B., McIntyre, A., 1990. Nutricline variation in the equatorial Atlantic coincident with the Younger Dryas. Paleoceanography 5, 997–1008.
- Moreno, A., Targarona, J., Henderiks, J., Canals, M., Freudenthal, T., Meggers, H., 2001. Orbital forcing of dust supply to the North Canary Basin over the last 250 kyr. Quatern. Sci. Rev. 20, 1327–1339.
- Morgan, M.E., Kingston, J.D., Marino, B.D., 1994. Carbon isotopic evidence for the emergence of C4 plants in the Neogene from Pakistan and Kenya. Nature 367, 162–165.
- Moritz, C., Patton, J.L., Schneider, C.J., Smith, T.B., 2000. Diversification of rainforest faunas: an integrated molecular approach. Ann. Rev. Ecol. Syst. 31, 533–563.
- Nicholson, S.E., 1996. A review of climate dynamics and climate variability in eastern Africa. In: Johnson, T.C., Odada, E.O. (Eds.), The Limnology, Climatology and Paleoclimatology of the East African lakes. Gordon and Breach Publishers, Amsterdam, pp. 25–56.
- Nicholson, S.E., 2000. The nature of rainfall variability over Africa on time scales of decades to millenia. Global Planet. Change 26, 137–158.
- Owen, R.B., 2002. Sedimentological characteristics and origins of diatomaceous deposits in the East African Rift system. SEPM Spec. Pub. 73, 233–246.
- Owen, R.B., Crossley, R., 1992. Spatial and temporal distribution of diatoms in sediments of Lake Malawi, Central Africa, and ecological implications. J. Paleolimnol. 7, 55–71.
- Owen, R.B., Renaut, R.W., Hover, V.C., Ashley, G.M., Muasya, A.M., 2004. Swamps, springs, and diatoms: wetlands of the semi-arid Bogoria-Baringo Rift, Kenya. Hydrobiologia 518, 59–78.
- Owen, R.B., Utha-aroon, C., 1999. Diatomaceous sedimentation in the Tertiary Lampang Basin, Northern Thailand. J. Paleolimnol. 22, 81–95.
- Paillard, D., Labeyrie, L., Yiou, P., 1996. Macintosh program performs Time-Series Analyses (AnalySeries 1.2 updated 2000). Eos, Transaction. AGU 77, 379.
- Pickford, M., 1975a. Late Miocene sediments and fossils from the northern Kenya Rift Valley. Nature 256, 279–284.
- Pickford, M., 1975b. Stratigraphy and palaeoecology of five late Cainozoic formations in the Kenya Rift Valley. Ph.D. Thesis, University of London.
- Pickford, M., 1978a. Geology, paleoenvironments and vertebrate faunas of the mid-Miocene Ngorara Formation, Kenya. In: Bishop, W.W. (Ed.), Geological background to fossil man. Geological Society of London/Scottish Academic Press, London, pp. 237–262.
- Pickford, M.H.L., 1978b. Stratigraphy and mammalian paleontology of the late-Miocene Lukeino Formation, Kenya. In: Bishop, W.W. (Ed.), Geological background to fossil man. Geological Society of London/Scottish Academic Press, London, pp. 263–278.
- Pickford, M., Johanson, D.C., Lovejoy, C.O., White, T.D., Aronson, J.L., 1983. A hominoid humeral fragment from the Pliocene of Kenya. Am. J. Phys. Anthropol. 60, 337–346.

- Pilbeam, D., 1989. Human Fossil History and Evolutionary Paradigms. In: Hecht, M.K. (Ed.), Evolutionary Biology at the Crossroads. Queens College Press, London, pp. 117–138.
- Pilskahn, C.H., 2004. Seasonal and interannual particle export in an African Rift Valley Lake: a 5-yr record from Lake Malawi, southern East Africa. Limnol. Oceanogr. 49, 964–977.
- Pilskahn, C.H., Johnson, T.C., 1991. Seasonal signals in Lake Malawi. Limnol. Oceanogr. 36 (3), 544–557.
- Pokras, E.M., Mix, A.C., 1985. Eolian evidence for spatial variability of late Quaternary climates in tropical Africa. Quatern. Res. 24, 137–149.
- Pokras, E.M., Mix, A.C., 1987. Earth's precession cycle and Quaternary climatic change in tropical Africa. Nature 326, 486–487.
- Potts, R., 1996. Evolution and climatic variability. Science 273, 922-923.
- Potts, R., 1998. Environmental hypotheses of hominin evolution. Yearb. Phys. Anthropol. 41, 93–136.
- Potts, R., Behrensmeyer, A.K., Ditchfield, P., 1999. Paleolandscape variation and early Pleistocene hominid activities: Members 1 and 7, Olorgesailie Formation, Kenya. J. Hum. Evol. 37, 747–788.
- Ravelo, A.C., Andreasen, D.H., Lyle, M., Lyle, A.O., Wara, M.W., 2004. Regional climate shifts caused by gradual global cooling in the Pliocene epoch. Nature 429, 263–267.
- Richerson, P.J., Bettinger, R.L., Boyd, R., 2005. Evolution of a restless planet: were environmental variability and environmental change major drivers of human evolution. In: Wuketits, F.M., Ayala, F.J. (Eds.), Handbook of Evolution. The Evolution of Living Systems (Including Hominids), vol. 2. Wiley-Verlag & Co., Weinheim, pp. 223–242.
- Rossignol-Strick, M., 1983. African monsoons, an immediate climate response to orbital insolation. Nature 304, 46–49.
- Rossignol-Strick, M., Nesteroff, W., Olice, P., Vergnaud-Grazzini, C., 1982. After the deluge: Mediterranean stagnation and sapropel formation. Nature 295, 105–110.
- Schefuß, E., Schouten, S., Jansen, J.H.F., Damasté, J.S.S., 2003. African vegetation controlled by tropical sea surface temperatures in the mid-Pleistocene. Nature 422, 418–421.
- Scholz, C.A., 2000. The Malawi Drilling Project: calibrating the record of climatic change from the continental tropics. GSA Abstracts with Programs, A–388.
- Semaw, S., Rogers, M.J., Quade, J., Renne, P.R., Butler, R.F., Dominguez-Rodfigo, M., Stout, D., Hart, W.S., Pickering, T., Simpson, S.W., 2003. 2.6-million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. J. Hum. Evol. 45, 169–177.
- Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K., Coppens, Y., 2001. First hominid from the Miocene (Lukeino formation, Kenya). C.R. Acad. Sci. Paris, Ser. IIa 332, 137–144.
- Shackleton, N., 1967. Oxygen isotope analyses and Pleistocene temperatures re-assessed. Nature 215, 15–17.
- Shackleton, N.J., Backman, J., Zimmerman, H., Kent, D.V., Hall, M.A., Toberts, D.G., Schnitker, D., Baldauf, J.G., Despraires, A., Homrighausen, R., Huddlestun, P., Keene, J.B., Kaltenback, J., Krumsiek, K.A.O., Morton, A.C., Murray, J.W., Westberg-Smith, J., 1984. Oxygen isotope calibration of the onset of ice-rafting and history of glaciation in the North Atlantic Region. Nature 307, 620–623.
- Sherwood, R.J., Ward, S.C., Hill, A., 2002b. The taxonomic status of the Chemeron temporal (KNM-BC 1). J. Hum. Evol. 42, 153–184.
- Sherwood, R.J., Ward, S., Hill, A., Duren, D.L., Brown, B., Downs, W., 2002a. Preliminary description of the *Equatorius africanus* partial skeleton (KNM-TH 28860) from Kipsaramon, Tugen Hills, Baringo District, Kenya. J. Hum. Evol. 42, 63–73.
- Stager, J.C., 1984. The diatom record of Lake Victoria (East Africa): the last 17,000 years. In: Mann, D.G. (Ed.), Proceedings of the Seventh Annual International Diatom Symposium. Strauss & Cramer, Koenigstein, pp. 455–476.
- Stager, J.C., Cummings, B., Meeker, L., 1997. A high-resolution 11,400-yr diatom record from Lake Victoria, East Africa. Quatern. Res. 47, 172–181.
- Stager, J.C., Cumming, B.F., Meeker, L.D., 2003. A 10,000-year high resolution diatom record of Pilkington Bay, Lake Victoria, East Africa. Quatern. Res. 59, 172–181.

- Stager, J.C., Mayewski, P.A., Meeker, L.D., 2002. Cooling cycles, Heinrich event 1, and the desiccation of Lake Victoria. Palaeogeogr. Palaeoclim. Palaeoecol. 183, 169–178.
- Stanley, S.M., 1985. Rates of evolution. Paleobiology 11, 13-26.
- Stanley, S.M., 1995. Climatic forcing and the origin of the human genus. In: Kennett, J., Stanley, S.M. (Eds.), Effects of past global change on life. National Academy of Sciences, Studies in Geophysics. National Academy Press, Washington, DC, pp. 233–243.
- Street-Perrott, F.A., Harrison, S.A., 1984. Temporal variations in lake levels since 30,000 yr BP — an index of the global hydrological cycle. In: Hansen, J.E., Takahashi, T. (Eds.), Climate Processes and Sensitivity. AGU, Washington, DC, pp. 118–129.
- Suwa, G., White, T.D., Howell, F.C., 1996. Mandibular postcanine dentition from the Shungura Formation, Ethiopia: crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. Am. J. Phys. Anthropol. 101, 247–282.
- Talling, J.F., 1986. The seasonality of phytoplankton in African lakes. Hydrobiologia 138, 139–160.
- Tattersall, I., Schwartz, J.H., 2000. Extinct Humans. Westview, Boulder, CO.
- Telford, R.J., Lamb, H.F., 1999. Groundwater-mediated response to Holocene climatic change recorded in the diatom stratigraphy of an Ethiopian crater lake. Quatern. Res. 52, 63–75.
- Thompson, L.G., Mosley-Thompson, E., Davis, M., Henderson, K.A., Brecher, H.A., Zagorodnov, V.S., Mashiotta, T.A., Lin, P.-N., Mikhalenko, V.N., Hardy, D.R., Beer, J., 2002. Kilimanjaro ice core records: evidence of Holocene climate change in tropical Africa. Science 298, 589–593.
- Tiedemann, R., Sarnthein, M., Shackleton, N.J., 1994. Astronomic timescale for the Pliocene Atlantic d¹⁸O and dust flux record of Ocean Drilling Program Site 659. Paleoceanography 9, 619–638.
- Tilman, D., Kilham, S.S., Kilham, P., 1982. Phytoplankton community ecology: the role of limiting nutrients. Ann. Rev. Ecol. Syst. 13, 349–372.
- Tobias, P.V., 1995. The brain of the first hominids. In: Changeux, J.P., Chavillon, J. (Eds.), Origins of the human brain. Clarendon Press, Oxford, pp. 61–81.
- Trauth, M.H., Deino, A.L., Bergner, A.G.N., Strecker, M.R., 2003. East African climate change and orbital forcing during the last 175 kyr BP. Earth Planet. Sci. Lett. 206, 297–313.
- Trauth, M.H., Maslin, M.A., Deino, A., Strecker, M., 2005. Late Cenozoic moisture history of East Africa. Science 309, 2051–2053.
- Valentine, J.W., 1984. Neogene marine climate trends: implications for biogeography and evolution of the shallow-sea biota. Geology 12, 647–659.
- van Dam, J.A., Aziz, H.A., Sierra, M.A.A., Hilgen, F.J., Ostende, L.W., van den Hoek, Lourens, L.J., Mein, P., van der Meulen, A.J.,

Pelaez-Campomanes, P., 2006. Long-period astornomical forcing of mammal turnover. Nature 433, 687-691.

- Verardo, D.J., Ruddiman, W.G., 1996. Late Pleistocene charcoal in tropical Atlantic deep-sea sediments: climatic and geochemical significance. Geology 24, 855–857.
- Verschuren, D., Laird, K., Cumming, B.F., 2000a. Rainfall and drought in equatorial east Africa during the past 1,100 years. Nature 403, 410–414.
- Verschuren, V., Tibby, J., Sabbe, K., Roberts, N., 2000b. Effects of depth, salinity, and substrate on the invertebrate community of a fluctuating tropical lake. Ecology 81, 164–182.
- Vrba, E.S., 1985. Ecological and adaptive changes associated with early hominid evolution. In: Delson, E. (Ed.), Ancestors: The Hard Evidence. Alan R. Liss, New York, pp. 63–71.
- Vrba, E.S., 1992. Mammals as key to evolutionary theory. J. Mammal. 73, 1-28.
- Vrba, E.S., 1995. On the connections between paleoclimate and evolution. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven, pp. 24–45.
- Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), 1995. Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven.
- Vrba, E.S., Denton, G.H., Prentice, M.L., 1989. Climatic influences on early hominid behavior. OSSA 14, 127–156.
- Walker, A.C., Leakey, R.E., Harris, J.M., Brown, F.H., 1986. 2.5 Myr Australopithecus boisei from west of Lake Turkana, Kenya. Nature 322, 517–522.
- Wallace, A.R., 1876. The Geographical Distribution of Animals. With a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface. I. Harper & Brothers, New York.
- Ward, S., Brown, B., Hill, A., Kelley, J., Downs, W., 1999. *Equatorius*: a new hominoid genus from the Middle Miocene of Kenya. Science 285, 1382– 1386.
- White, T., 2003. Early hominids diversity or distortion. Science 299, 1994– 1997.
- Williams, L.A.J., Chapman, G.R., 1986. Relationships between major structures, salic volcanism and sedimentation in the Kenya Rift from the equator northwards to Lake Turkana. In: Frostick, L.E., Renaut, R.W., Reid, I., Tiercelin, J.J. (Eds.), Sedimentation in the African Rifts. Geol. Soc. London, Spec. Pub., No. 25, pp. 59–74.
- Wood, B., 1992. Origin and evolution of the genus *Homo*. Nature 355, 783-790.
- Wood, B., 1994. The oldest hominid yet. Nature 371, 280-282.
- Wood, B., 2002. Hominid revelations from Chad. Nature 418, 133-135.
- Wood, B.A., Richmond, B.J., 2000. Human evolution: taxonomy and paleobiology. J. Anat. 196, 19–60.