The First Humans - Origin and Early Evolution of the Genus *Homo*

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Chapter 13
Plio-Pleistocene East African Pulsed Climate Variability and Its Influence on Early Human Evolution

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Introduction

Long-term climate change seems to be modulated primarily by tectonic changes at both the global and local scale (Maslin et al., 2001). Late Cenozoic global cooling has been ascribed to both the uplift of Tibet (Ruddiman and Raymo, 1988), and the closure of the Panama Isthmus (Haug and Tiedemann, 1998), although the exact role of atmospheric carbon dioxide is still unclear (Sundquist and Visser, 2004). In East Africa, long-term climate change is also controlled by local tectonics, especially the dynamic development of the branching East African Rift System (Sepulchre et al., 2006). Early hominin evolution in East Africa thus occurs at the same time as both long-term global cooling and extensive local tectonic changes. There is a compelling need to understand how these two environmental factors interact at the local scale and affect flora and fauna living in the East African Rift. The geologic record of the last 5 million years demonstrates that both local and global influences can lead to extremely rapid environmental change (Maslin and Christensen, 2007).

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East African Tectonic History

The East African Rift System (EARS) is one of the most extensive geological features on the Earth's surface, running North-South for approximately 4,500 km from Syria through East Africa to Mozambique. Volcanism associated with the EARS began as early as 45–33 Ma in the Ethiopian Rift, by 33 Ma in northern Kenya, and by 15–8 Ma in the central and southern segments of the rift in Kenya and Tanzania (Fig. 13.1).

The early stages of rifting were characterized by updoming and downwarping, while subsequent faulting progressed from north to south (Fig. 13.1). Major faulting in Ethiopia between 20–14 Ma was followed by the generation of East dipping faults in northern Kenya between 12 and 7 Ma, and superseded by normal faulting on the western side of the central and southern Kenya Rift between 9 and 6 Ma (Baker et al., 1988, Strecker et al., 1990; Ebinger et al., 2000). These early half grabens were subsequently antithetically faulted between about 5.5 and 3.7 Ma, leading to a full-graben morphology (Baker et al., 1988, Strecker et al., 1990). This full-graben stage was preceded by the formation of the large Aberdare volcanic complex with elevation in excess of 4,000 m, forming an important orographic barrier in Kenya by ~5 Ma (Williams et al., 1983). By 2.6 Ma, the graben was further segmented in the central Kenya Rift by west-dipping faults, creating the 30 km wide intrarift Kinangop Plateau and the tectonically active 40-km-wide inner rift (Fig. 13.1) (Baker et al., 1988; Strecker et al., 1990; Bosworth and Strecker, 1997). In the Tanzanian sector of the rift, sedimentation in isolated basins began at ~5 Ma (Foster et al., 1997). A major phase of rift faulting occurred at 1.2 Ma and produced the present-day rift escarpments (Foster et al., 1997).

Plio-Pleistocene Variations in East African Moisture Availability

Figure 13.1 illustrates that late Cenozoic tectonic activity in the EARS led to the production of isolated basins within

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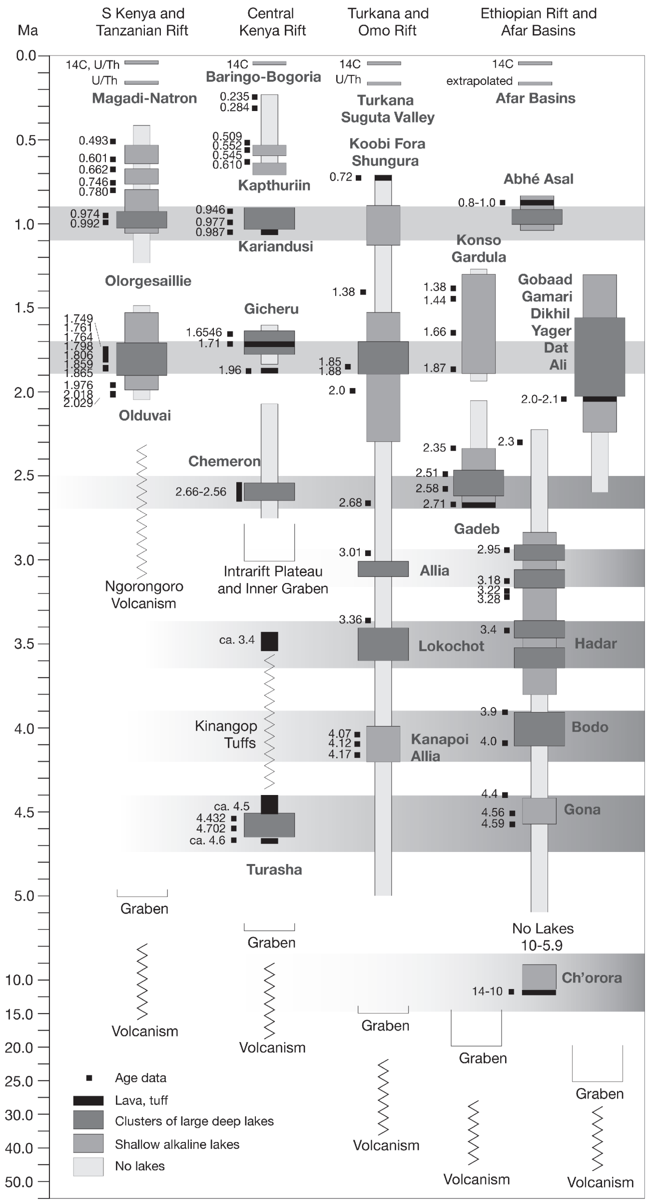

Fig. 13.1 Compilation of tectonic features and prominent lake periods for the eastern branch of the East African Rift System. Tectonic features and events complied from Baker et al. (1988), Strecker et al. (1990), Ebinger et al. (2000), Williams et al. (1983) and Foster et al. (1997). Paleoenvironmental and radiometric age data for the Olduvai Basin from Walter et al. (1991) and Ashley and Hay (2002); for the Magadi-Natron and Olorgesailie Basins from Potts (1998,1999), and Behrensmeyer et al. (2002). Natron has one persistent lacustrine interval (a Member of the Monik Formation, called the Moinik Clays) dated to 1.1–1.0 Ma (Deino, A., pers. comm., 2008). Paleoenvironmental and radiometric age data for the Gicheru Basin from Baker et al. (1988), Strecker (1991), Boven (1992) and this work; for the Naivasha Basin from Strecker et al. (1990) and Trauth et al. (2003, 2005); for the Nakuru-Elmenteita Basin from Evernden and Curtis (1965), Strecker (1991), Boven (1992) and Trauth et al. (2005); for the Baringo-Bogoria Basin from Owen et al. (2002) and Deino et al.(2006); for the Suguta Basin from Butzer et al.(1969), Hillarie-Marcel et al. (1986) and Sturchio et al. (1993); for the Omo-Turkana Basin from McDougall and Watkins (1988) and Brown and Feibel (1991); for the Ethiopian Rift from Williams et al. (1979), Gasse (1990) and WoldeGabriel et al. (2000); for the Afar Basin from Gasse (1990).

which lakes could form. Southward propagation of rifting and magmatic activity resulted in formation of lake basins first in the northern parts of the EARS. For example, the fluviolacustrine history of the Afar, Omo-Turkana and Baringo-Bogoria Basins in the north began in the Middle and Late Miocene, whereas the oldest lacustrine sequences in the central and southern segments of the rift in Kenya and Tanzania occur in the Early Pliocene (Tiercelin and Lezzar, 2002). In general, palaeo-lakes first appear in the EARS earlier in the north than in the south, due to the progressive formation of separate basins. If tectonics were the sole control over lake formation, then either a North to South or Northwest to Southeast temporal trend would be expected. However, what is observed is the appearance of large, deep lakes synchronously across large geographical areas at specific points in time (Trauth et al., 2005, 2007), suggesting that regional climatic control is operative.

Carbon isotope records from both soil carbonates (Levin et al., 2004; Wynn, 2004; Segalen et al., 2007) and biomarkers (*n*-alkanes) extracted from deep-sea sediments (Feakins et al., 2005) provide clear evidence a progressive vegetation shift from C_3 (~trees and shrubs) to C_4 (~tropical grasses) plants during the Plio-Pleistocene. This shift has been ascribed to increased aridity that arose from the progressive rifting of East Africa (deMenocal, 2004; Sepulchre et al., 2006). Superimposed on this regime of subdued moisture availability, three periods characterized by the occurrence of large and deep lakes have been broadly identified in East Africa at 2.7–2.5, 1.9–1.7 and 1.1–0.9 Ma (Trauth et al., 2005, 2007), indicating consistency in the moisture history of the Kenyan and Ethiopian Rifts. Although preservation of East African lake records prior to 2.7 Ma is patchy, there is limited evidence for lake phases at ~3.20–2.95, ~3.4–3.3, 4.0–3.9, and ~4.7–4.3 Ma (Fig. 13.1). The lake phases correspond to drops in the East Mediterranean marine dust abundance (Larrasoaña et al., 2003), which are thought to reflect the aridity of the eastern Algerian, Libyan, and western Egyptian lowlands located north of the central Saharan watershed (Fig. 13.2). The lake phases also correspond to an increased occurrence of sapropels in Mediterranean Sea, which are thought to be caused by increased Nile River discharge (Lourens et al., 2004). The correspondence of the Mediterranean marine records with lake records of East Africa suggest a consistent moisture record for a region encompassing much of central and northern Africa over the last 3–5 million years.

In contrast, these East African wet phases correlate with significant intermediate-term increases in the dust records from ocean sediment cores adjacent to West Africa and Arabia (deMenocal, 1995, 2004). While, at first, this seems contradictory, examination of these data in chronologic detail demonstrates that both the lake and dust records are responding to precessional forcing, and that they are in-phase.

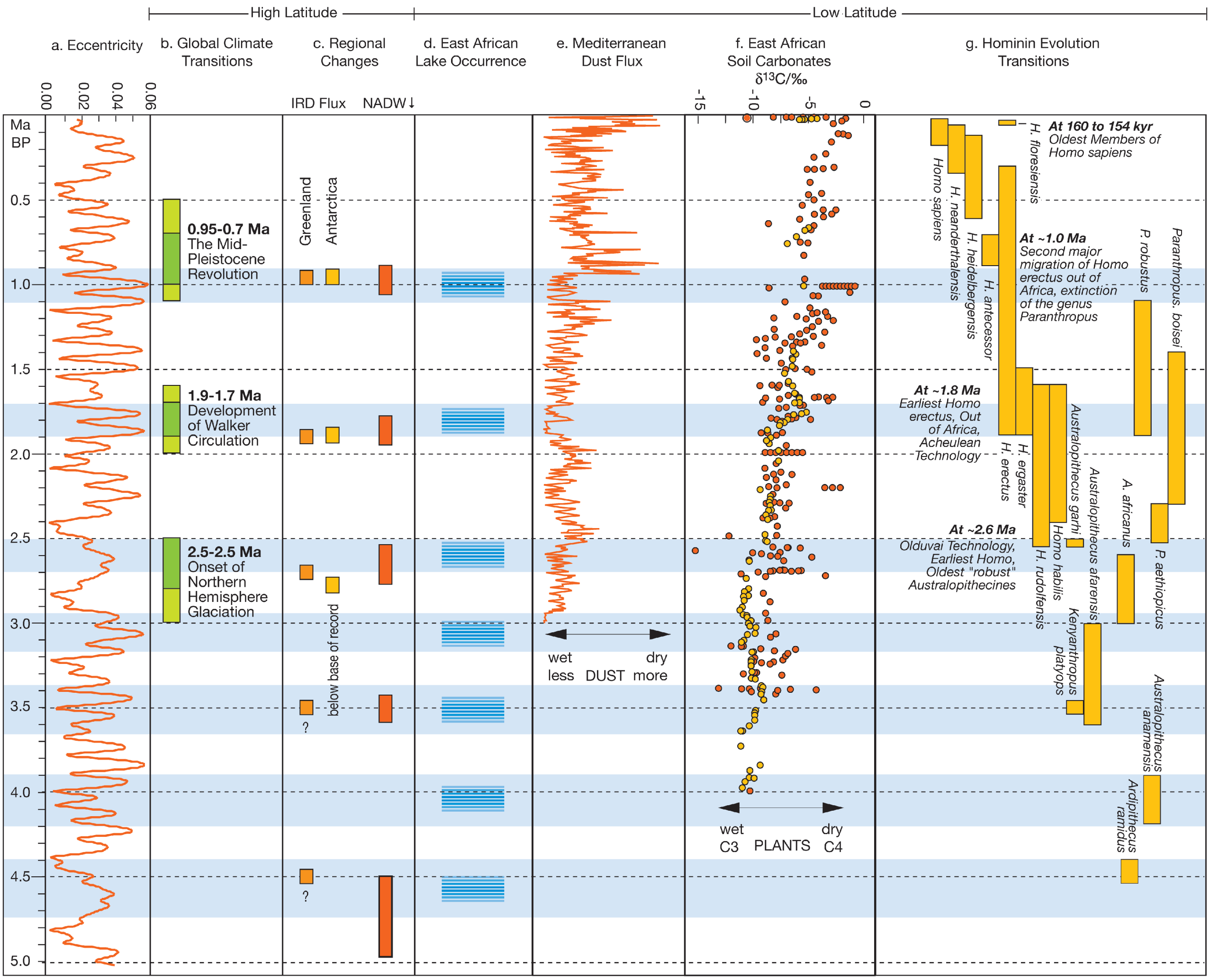

Fig. 13.2 Comparison of eccentricity variations (Berger and Loutre, 1991) with high latitude climate transitions (St John and Krissek, 2002; Cowan, 2001) and Mediterranean dust flux (Larrasoaña et al., 2003). Soil carbonate carbon isotopes: (yellow dots = Levin et al., 2004; red dots = Wynn et al., 2004). Data for East African lake occurrences from Trauth et al. (2005, 2007). Hominin species appearances and durations from Reed (1997), Dunsworth and Walker (2002), McHenry (2002), White (2002) and White et al. (2006).

Deino et al., (2006) and Kingston et al., (2007) found that the major lacustrine episode of the Baringo Basin between 2.7–2.55 Ma actually consisted of five paleo-lake phases separated by a precessional cyclicity of 23 kyr. The lakes occurrences are in-phase with increased freshwater discharge, and therefore sapropel formation in the Mediterranean Sea (Lourens et al., 2004), and are out of phase with the dust records from the Indian Ocean (deMenocal, 1995, 2004). Hence, the lake records from East Africa and the Indian Ocean dust records document extreme climate variability with precession-forced wet and dry phases. Precessional forcing of vegetation change also occurred at this time in southwest Africa, independent of glacial-interglacial cycles (Denison et al., 2005). There is also emerging evidence for precessional forcing of the 1.9–1.7 Ma lake phase in the KBS Member of the Koobi Fora Formation in the northeast Turkana Basin of Kenya (Lepre et al., 2007). During the same period, an oxygen isotope record from the Buffalo Cave flowstone (Makapansgat Valley, Limpopo Province, South Africa) shows clear evidence of precessionally-forced changes in rainfall in South Africa (Hopley et al., 2007).

Orbital-Forcing of African Climate

There is a growing body of evidence for precession-forcing of moisture availability in the tropics, in East Africa during the Pliocene (deMenocal, 1995, 2004; Deino et al., 2006; Kingston et al., 2007; Hopley et al., 2007; Lepre et al., 2007), and elsewhere in the tropics during the Pleistocene (Bush et al., 2002; Trauth et al., 2003; Cruz et al., 2005; Wang et al., 2004). The precessional control on tropical moisture has also been clearly illustrated by the climate modelling of Clement et al. (2004), which showed that a 180° shift in precession could change annual precipitation in the tropics by at least 180 mm/year and cause a significant shift in seasonality. Support for increased seasonality during these extreme periods of climate variability also comes from mammalian community structures (Reed, 1997; Bobe and Eck, 2001) and hominin paleo-diet reconstructions (Teaford and Ungar, 2000).

The late Cenozoic periods of extreme climate variability appear to correlate with maxima in the 400 kyr component of the earth's eccentricity cycle. Prior to 2.7 Ma the wet phases appear every 400 ka (see Fig. 13.1). After 2.7 Ma, however, the wet phases appear every 800 ka, with periods of precessional-forced extreme climate variability at 2.7–2.5, 1.9–1.7 and 1.1–0.9 Ma before present, whereas other periods of eccentricity maxima at ~2.2, ~1.4 and ~0.6 Ma are not associated with the alternating formation of large lakes or increased dust. The three late Cenozoic lake phases do, however, correlate with significant global climatic transitions as well as peaks in eccentricity. Hence after 2.7 Ma, global climate changes seem to be required to cause an increased regional climate sensitivity to precessional-forced insolation and increased seasonality, which allows either large deep lakes to develop or causes extreme aridity and large dust loads to the adjacent oceans. In contrast, prior to 2.7 Ma, eccentricity maxima alone were sufficient to produce regional sensitivity. It remains to be determined whether the long-term drying trend in East Africa, or the global cooling trend is responsible for this shift from a simple linear response to long-term eccentricity forcing.

Global Climate Transitions

The last three major Plio-Pleistocene lake phases correspond to global climate transitions. The lake phase at 2.7–2.5 Ma corresponds to intensification of the Northern Hemisphere Glaciation (INHG) (Haug and Tiedemann, 1998), that at 1.9–1.7 Ma to development and significant intensification of the Walker Circulation (Ravelo et al., 2004), and that at 1.1–0.9 Ma to initiation of the Mid-Pleistocene Revolution (Berger and Jansen, 1994). Each of these global climate transitions was accompanied by reduced North Atlantic Deep Water (NADW) formation (Haug and Tiedemann, 1998) and increased ice rafting from both Greenland and Antarctica (St. John and Krissek, 2002; Cowan, 2001). Ice expansion and cooling in either hemispheres would have significantly increased the Pole-Equator thermal gradient, leading to a northern and/or southern compression of the Intertropical Convergence Zone (ITCZ). A similar effect occurred during the Last Glacial Maximum, where a strong compression of the ITCZ is observed both in paleo-reconstructions of tropical hydrology (e.g., Peterson et al., 2000; Chiang et al., 2003; Wang et al., 2005), and *via* climate modelling (Lautenschlager and Herterich, 1990; Bush and Philander, 1999; Bush, 2001). Most important for East Africa moisture availability is the compression of the northern Hemisphere component of the ITCZ because it influences the strength of the SE Asian monsoons. Compression of the ITCZ is thus an essential component to increasing the sensitivity of East Africa to precessional forcing of moisture availability; otherwise moisture is transported north and south away from the Rift Valley. Along the whole length of the rift, without this high-latitude climate control, East Africa cannot receive enough rainfall to fill large deep freshwater lakes during positive precessional periods. Hence after 3 Ma, it seems that both global climate forcing and eccentricity maxima are required to generate episodes of extreme precessional forced climate.

Climate Variability and Early Human Evolution

On time scales of more than 100 kyr, rift-related volcano-tectonic processes shaped the landscape of East Africa and profoundly influenced local climate and surface hydrology through the development of relief. Through uplift of the Kenyan and Ethiopian Plateaus, changes in orography and associated rain shadow are believed to be the major driving force for increased variability of moisture availability throughout Eastern Africa. This increased sensitivity has resulted in a modern Rift Valley that hydrological modelling suggests could support lakes as deep as 150 m with an annual precipitation increase of only 15–30% (Bergner et al., 2003). Prior to the INHG there is a linear relationship between long-term eccentricity variations and the development of deep freshwater lakes in the East African Rift. From the ONHG onwards, global climate transitions, which resulted in an increased Pole-Equator gradients and compression both north and south boundaries of the ITCZ, were required to make East African moisture availability sensitive to maxima in eccentricity and thus changes in precession.

The alternating extreme wet and dry periods would have had a profound affect on the climate and vegetation of East Africa. The sinusoidal precessional forcing at the equator consists of periods of less than 2,000 years, during which 60% of total variation in daily insolation and seasonality occurs. These are followed by ~8,000 years when relatively little change in daily insolation occurred (Maslin et al., 2005; Maslin and Christensen, 2007). Hence, instead of precession being a smooth forcing, it combines rapid strong forcing with long periods of relatively weak forcing. Rapid stratigraphic transitions from deep lacustrine to fluvial deposition associated with the diatomite Pliocene lakes deposits in the Baringo Basin suggests that this sinusoidal precessional-forcing caused lakes to appear rapidly, remain part of the landscape for thousands of years, then disappear rapidly (Deino et al., 2006; Kingston et al., 2007). In fact, the absence of shallow-water diatom species from key Plio-Pleistocene lake deposits (Deino et al., 2006; Kingston et al., 2007) suggests that these lakes could have dried up in less than 500 years. This has important implications for the speciation and dispersal of mammals (including hominins) in East Africa. Figure 13.2 shows that between 5.0 and 0.5 Ma, the periods of highly variable East African climate – those oscillating from very wet to very dry (indicated by the striped blue boxes in Fig. 13.2d) – occupied less than a third of the total time. In contrast, 12 out of the 15 hominin species (~80%) first appeared in one of these extreme 'wet-dry' periods. In particular there seems to be a strong correspondence between these extreme climate periods and the appearance of appearance of such species as *Homo habilis*, *H. rudolfensis*, *H. erectus* and/or *H. ergaster* (See Fig. 13.2g). Even taking into the account the great difficulty in dating the first appearance of African hominins, and the problem of pseudo-speciation events (Vrba, 1993; Smith, 1994), this is compelling evidence for the preferential evolution of hominins during extreme climate periods. What we cannot rule out or account for is the possibility that the increased moisture availability during the periods increases the likely preservation of fossils and thus produces a false correlation.

Linking African Lake Variability and Theories of Human Evolution

We suggest that ephemeral lakes, expanding and contracting on precessional timescales, would have evoked wide-spread, regional-scale, rapid, and extreme environmental variability. However, the difficulty in invoking orbital forced changes in local hydrology arises not out of the question of scale, but of timing: what part of these climate variations may have influenced the speciation and extinction events? Figure 13.3 presents three different models of the lake response to local orbital forcing.

The first model suggests that there is a relatively smooth, gradual transition between periods with deep lakes and periods without lakes. If this 'smooth' model is correct, then there may have been prolonged periods of wet and arid conditions, which may invoke the Red Queen or the Turnover Pulse Hypothesis (TPH) as possible causes of evolution (Van Valen, 1973; Vrba, 1993). Alternatively, there may have been non-linear dynamic changes related to the complex interaction of precipitation, temperature, and seasonality patterns that produced threshold changes in the local vegetation which may have influenced evolution (Maslin, 2004).

The second model is a 'threshold' model, so, instead of a smooth gradual transition from wet and drier condition, the ephemeral lakes expanded and contracted extremely rapidly, producing a wide-spread, regional-scale, rapid, and extreme environmental variability, required by the Variability Selection Hypothesis of human evolution (Potts, 1998). Model three is a more extreme example of the threshold model, in which there is 'extreme climate variability' during the rapid transition from deep-lake to no-lake phases. This would provide extreme short-term variability that could influence speciation and extinction events, especially if this climate change occurred over a large geographic region.

There is, of course, a fourth possibility, namely that all three models contain prolonged extreme wet and dry periods, which would have provided prolonged periods of either extremely abundant or scarce water and food resources. The extreme dry periods would support a model such as the TPH. In contrast, the extreme wet periods, with very deep freshwater lakes, are rare events in the paleoclimatic history of East Africa. As such, speciation events may have occurred in the high energy/high competition environments provided by the wet periods. This would conform to the Red Queen Hypothesis.

At present, the preliminary data from Lake Baringo (Kingston et al., 2007) suggest the diatomites are typically bracketed by 20–30 cm of fine sand and silt horizons containing fish fossils. These grade into high-energy terrestrial facies, indicating relatively rapid cycling between deep lake and fully subaerial conditions. This suggests that for this region, at least, model three – extreme climate variability – is the most likely. What is now required are high resolution paleoclimate data with which to test the different models outlined above. There are also other methods for testing which of the three theoretical models is closest to reality. First, oxygen isotopes of the diatoms in the lake sediment can be analyzed, as these provide a measure of the evaporation-precipitation balance of the whole lake. This, in turn, provides an estimate of how quickly the lake was expanding and contracting. Second, one of us (MT) has already sampled the Late Glacial – Early Holocene paleo-lake in the Suguta Valley of northern Kenya, and its appearance and disappearance has been dated using radiocarbon (Garcin et al., 2009). This will yield an accurate estimate of how quickly recent lakes can vary providing an analog for the older material.

The Pulsed Climate Variability Hypothesis

In summary, new paleoclimate data suggest that the long-term drying trend in East Africa was punctuated by episodes

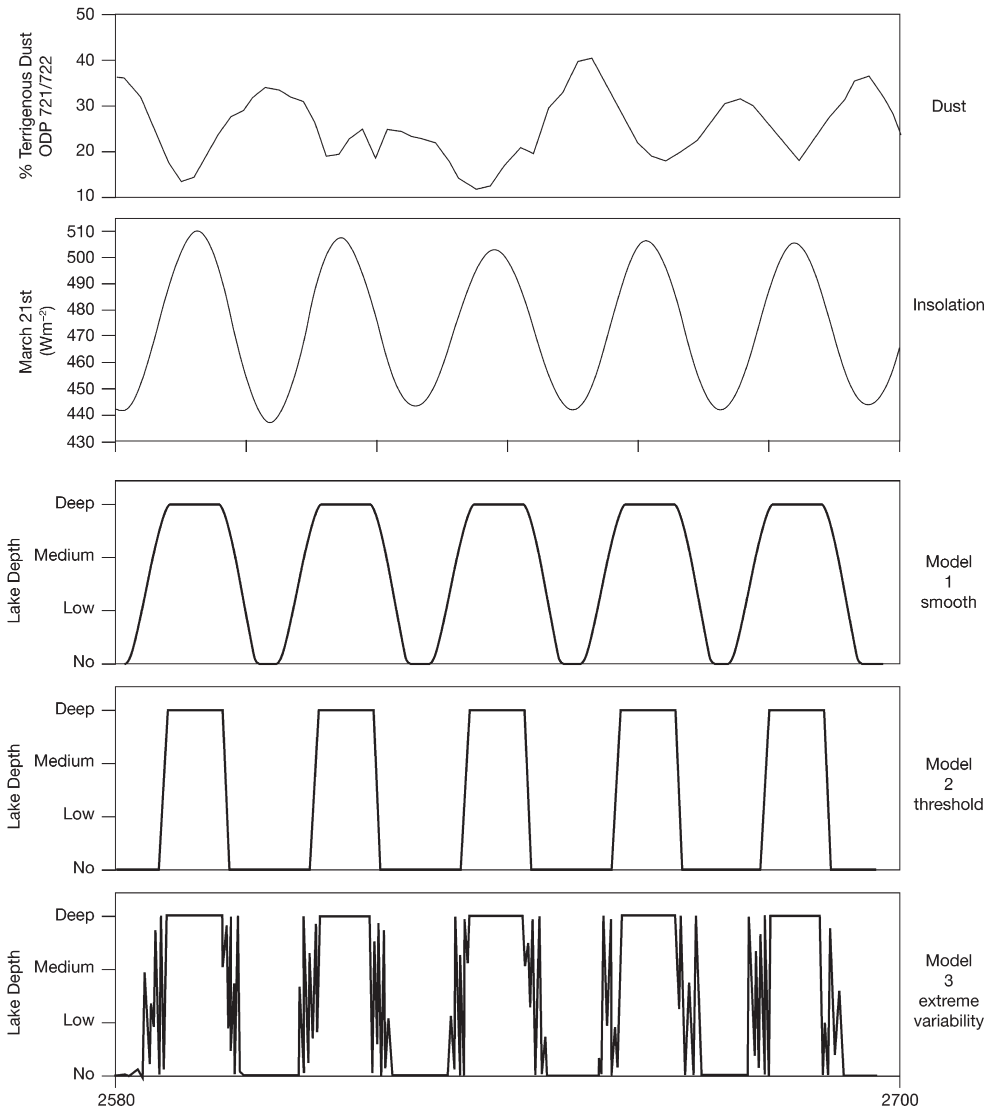

Fig. 13.3 Three theoretical models of lake changes in East Africa during the Plio-Pleistocene. Model 1: 'smooth' and relatively slow transitions from *deep* to *no* lake conditions, which would imply that either high energy wet conditions or prolonged aridity may have influenced human evolution. Model 2: 'threshold' rapid transitions from *deep* to *no* lake conditions, which would imply that rapid transition may have influenced human evolution, or the high energy wet conditions or prolonged aridity as suggested by Model 1. Model 3: 'extreme variability,' with high variability during the transitions between *deep* and *no* lake conditions, which implies variability influenced human evolution or, again, either high energy wet conditions or prolonged aridity.

of short, alternating periods of extreme humidity and aridity. These periods of 'pulsed climate variability' are characterized by the precession-forced appearance and disappearance of large, deep lakes in the East African Rift Valley, and are paralleled by low and high wind-driven dust loads reaching the adjacent ocean basins. During the last 3 million years, such periods only occur at the times of major global climatic transitions, such as the intensification of Northern Hemisphere Glaciation (2.7–2.5 Ma), development of the Walker circulation (1.9–1.7 Ma), and the Mid-Pleistocene Revolution (1.0–0.7 Ma). We suggest that high latitude forcing in both hemispheres is required to compress the Inter-Tropical Convergence Zone so that East Africa becomes locally sensitive to precessional forcing, resulting in rapid shifts from wet to dry conditions. Building on Potts' (1998) variability selection hypothesis, we suggest that these periods of pulsed climate variability may have provided a catalyst for evolutionary change, and driven key speciation and dispersal events amongst mammals and hominins in Africa. Hominin species, in particular the early species attributed to the genus *Homo*, seem to differentially originate and go extinct during periods of extreme climate variability. Results presented in this paper may represent the basis of a new theory of early human evolution in Africa.

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