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Invited review

East African climate pulses and early human evolution

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ABSTRACT

Current evidence suggests that all of the major events in hominin evolution have occurred in East Africa. Over the last two decades, there has been intensive work undertaken to understand African palaeoclimate and tectonics in order to put together a coherent picture of how the environment of East Africa has varied in the past. The landscape of East Africa has altered dramatically over the last 10 million years. It has changed from a relatively flat, homogenous region covered with mixed tropical forest, to a varied and heterogeneous environment, with mountains over 4 km high and vegetation ranging from desert to cloud forest. The progressive rifting of East Africa has also generated numerous lake basins, which are highly sensitive to changes in the local precipitation-evaporation regime. There is now evidence that the presence of precession-driven, ephemeral deep-water lakes in East Africa were concurrent with major events in hominin evolution. It seems the unusual geology and climate of East Africa created periods of highly variable local climate, which, it has been suggested could have driven hominin speciation, encephalisation and dispersal out of Africa. One example is the significant hominin speciation and brain expansion event at ~1.8 Ma that seems to have been coeval with the occurrence of highly variable, extensive, deep-water lakes. This complex, climatically very variable setting inspired first the *variability selection hypothesis*, which was then the basis for the *pulsed climate variability hypothesis*. The newer of the two suggests that the long-term drying trend in East Africa was punctuated by episodes of short, alternating periods of extreme humidity and aridity. Both hypotheses, together with other key theories of climate-evolution linkages, are discussed in this paper. Though useful the actual evolution mechanisms, which led to early hominins are still unclear and continue to be debated. However, it is clear that an understanding of East African lakes and their palaeoclimate history is required to understand the context within which humans evolved and eventually left East Africa.

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1. Introduction

Human evolution is characterised by speciation, extinction and dispersal events that have been linked to both global and/or regional palaeoclimate records (deMenocal, 1995; Trauth et al., 2005; Carto et al., 2009; Castañeda et al., 2009; Armitage et al., 2011; Donges et al., 2011; Shultz et al., 2012). However, none of these records fully explain the timing or the causes of these human evolution events (Maslin and Christensen, 2007; Trauth et al., 2009; Potts, 2013). This is primarily due to global and regional palaeoclimate records not being representative of the climate of the East Africa (Shultz and Maslin, 2013). Understanding the climate of East Africa is essential because, despite the dispersal of hominins out of Africa after two million years ago (Agusti and Lordkipanidze, 2011) current evidence suggests the majority of hominin species originated in East Africa (Antón and Swisher, 2004; Wood, 2014).

Environmental pressures have long been assumed to play a key role in hominin speciation and adaptation (Maslin and Christensen, 2007) and a number of iconic theories have been developed to frame and develop the discussion of hominin evolution. Table 1 tries to put these key theories into the context of overarching evolutionary theory. Though the split between *phylogenetic gradualism* and *punctuated equilibrium* is artificial it does provide a starting point with which to discuss theories of early human evolution. In Table 1, gradualism has been split into constant and variable evolution rates to reflect the full range of current opinions;

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Table 1
Early human evolutionary theories placed in the context of overall evolutionary theory and modes of climatic change.

EVOLUTIONARY FORM		CLIMATE STRESS: None	Long-term state change	Threshold event	Variability
Phyletic Gradualism	constant	Red Queen (Van Valen 1973)	*Allopatic speciation*		
Phyletic Gradualism	variable	Red Queen (Van Valen 1973)	Turnover-pulse hypothesis (Vrba 1985) Savannah hypothesis	*Allopatic speciation*	Variability selection hypothesis (Potts 1998) Pulsed-climate variability hypothesis (Maslin & Trauth 2009)
Puncuated Equilibrium		Court Jester (e.g. Impact event) (Bamosky 2001)	Aridity hypothesis (de Menocal 1995)	Court Jester (Bamosky 2001) *Allopatic speciation*	Pulsed-climate variability hypothesis (Maslin & Trauth 2009)

though attempts have been made to combine *phylogenetic gradualism* and *punctuated equilibrium*, such as *punctuated gradualism* (Malmgren et al., 1983), these have not been included as they are not widely accepted.

The first key environmental theory to explain bipedalism was the *savannah hypothesis*, which suggested that hominins were forced to descend from the trees and adapted to life on the savannah facilitated by walking erect on two feet (Lewin and Foley, 2004). This theory was refined as the *aridity hypothesis*, which suggested that the long-term trend towards increased aridity and the expansion of the savannah was a major driver of hominin evolution (deMenocal, 1995, 2004; Reed, 1997). A key addition to this theory was the suggestion that during periods when aridification accelerated, due to thresholds in the global climate system, then thresholds in evolution were reached and major hominin speciation events occurred (deMenocal, 1995).

The *turnover pulse hypothesis* (Vrba, 1988) was originally developed to explain discrete patterns in ungulate speciation, and suggests that acute climate shifts drove adaptation and speciation. Vrba (1988) recognised that environmentally-induced extinctions hurt specialist species more than generalist species. Hence when there is an environmental disruption, the generalists will tend to thrive by utilizing new environmental opportunities and by moving elsewhere to take advantage of other areas that have lost specialist species. The specialists will experience more extinctions, and therefore an increased speciation rate within their group. This would lead to more rapid evolution in isolated areas, i.e., allopatric speciation, whereas the generalists will become more spread out.

The *variability selection hypothesis* advocates the role of environmental unpredictability in selecting for behavioural or ecological flexibility (Potts, 1998, 2013; Grove, 2011a,b). This theory develops the original *turnover pulse hypothesis* but instead splits species into their varying ability to adapt and evolve to a more variable and unpredictable environment. The *variability selection hypothesis* emphasises the long-term trends toward a drier and more variable climate. It however struggles to explain the current palaeoanthropological evidence that suggests a pulsed/threshold nature of hominin speciation and migration events. A direct development of the *variability selection hypothesis* is the *pulsed climate variability hypothesis*, which highlights the role of short periods of extreme climate variability specific to East Africa in driving hominin evolution (Maslin and Trauth, 2009). It is the palaeoclimate evidence for this later framework, the *pulsed climate variability hypothesis*, which is discussed in this review along with how the other evolutionary theories may be applied given the new context (see Fig. 1).

2. Formation and development of the East Africa rift system

On a regional scale, tectonics can cause significant changes in climate, hydrology and vegetation cover. In East Africa, long-term climatic change is controlled by tectonics, with the progressive formation of the East African Rift Valley leading to increased aridity and the development of fault graben basins as catchments for lakes (Fig. 2). Rifting begins with updoming at the site of future separation, and downwarping away from the site. This is followed by rifting and separation as half grabens (land that has subsided with a fault on one side) are formed on either side of the rift. While the early stages of rifting in East Africa were characterised by general updoming and downwarping, faulting during the later stages progressed from north to south.

Volcanism in East Africa may have started as early as 45–33 Ma in the Ethiopian Rift (Trauth et al. (2005, 2007) while initial uplift may have occurred between 38 and 35 Ma (Underwood et al., 2013). There is evidence for volcanism as early as 33 Ma in northern Kenya, but magmatic activity in the central and southern rift segments in Kenya and Tanzania did not start until between 15 and 8 Ma (e.g., Bagdasaryan et al., 1973; Crossley and Knight, 1981; McDougall and Watkins, 1988; George et al., 1998; Ebinger et al., 2000). The high relief of the East African Plateau developed between 18 Ma and 13 Ma (Wichura et al., 2010). Major faulting in Ethiopia occurred between 20 and 14 Ma and was followed by the development of east-dipping faults in northern Kenya between 12 and 7 Ma (Fig. 3). This was superseded by normal faulting on the western side of the Central and Southern Kenya Rifts between 9 and 6 Ma (Baker et al., 1988; Blisniuk and Strecker, 1990; Ebinger et al., 2000). Subsequent antithetic faulting of these early half grabens between about 5.5 and 3.7 Ma then generated a full-graben (a block of subsided land with faults on either side) morphology (Baker et al., 1988; Strecker et al., 1990). Prior to the full-graben stage, the large Aberdare volcanic complex (elevations in excess of 3500 m), an important Kenyan orographic barrier, was established along a section of the eastern rim of the EARS (Williams et al., 1983). By 2.6 Ma, the Central Kenyan Rift graben was further segmented by west-dipping faults, creating the 30-km-wide intrarift Kinangop Plateau and the tectonically active 40-km-wide inner rift (Baker

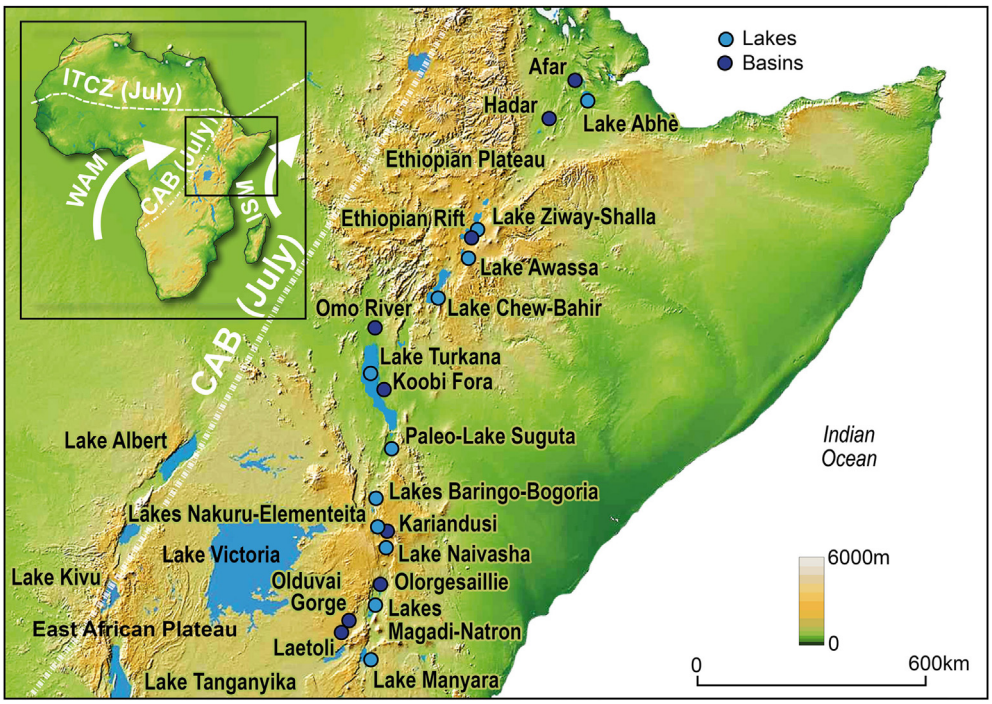

Fig. 1. Map of East Africa with main modern lake and palaeolake Basins (adapted from Junginger and Trauth, 2013).

et al., 1988; Strecker et al., 1990). After 2 Ma, many of the Kenyan lake basins continued to fragment due to ongoing volcanic activity. This includes the formation of the Barrier volcano separating Lake Turkana and the Suguta Valley (~1.4 Ma eastern side and ~0.7 Ma western side) and the Emuruangogolak volcano (~1.3 Ma) that separate Lake Baringo and the Suguta Valley (Dunkley et al., 1993; McDougall et al., 2012). Therefore before 1.4 Ma, an inter-connected lake system may have existed stretching from the Omo National Park in the north to just north of Lake Baringo in the south (Fig. 2). In the Tanzanian sector of the rift, sedimentation in isolated basins began at ~5 Ma. A major phase of rift faulting occurred at 1.2 Ma resulting in the present-day rift escarpments (Foster et al., 1997).

Tectonic events such as these are associated with a variety of biotic changes. Over the Oligocene and Miocene progressive uplift of East Africa split the pan-Africa rainforest which joined the Congo with East Africa resulting in endemic species in East Africa emerging at 33, 16 and 8 Ma (Couvreur et al., 2008). During the Plio-Pleistocene, there is evidence from soil carbonates (Levin et al., 2004; Wynn, 2004; Ségalen et al., 2007; Levin, 2013), marine sediment *n*-alkane carbon isotopes (Feakins et al., 2005, 2007; 2013) and fossilised mammal teeth (Harris et al., 2008; Brachert et al., 2010) that there was a progressive vegetation shift from C_3 plants to C_4 plants during the Pliocene and Pleistocene. This vegetation shift has been ascribed to increased aridity due to the progressive rifting and tectonic uplift of East Africa (deMenocal, 2004). The only data set that disagrees with this overall aridity trend is pollen data from DSDP Site 231 in the Gulf of Aden (Bonnefille, 2010; Feakins et al., 2013). These data suggest that the amount of grass pollen decreased over the last 12 Myrs but that there was little change between 2 and 4 Ma. However, this is a

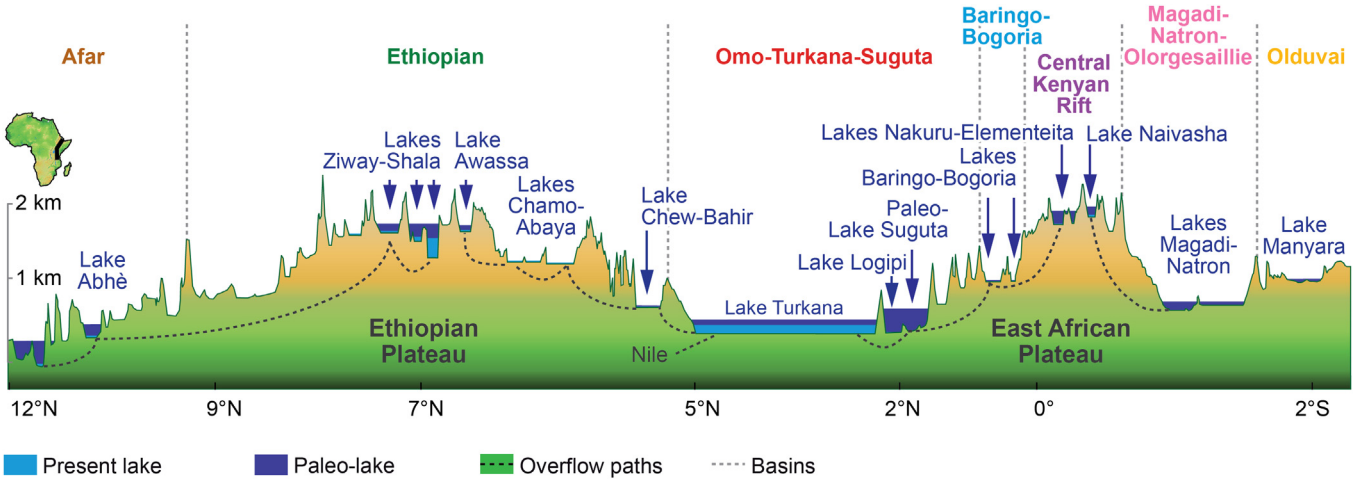

Fig. 2. Cross section of East Africa showing the main modern lake and palaeolake Basins (adapted from Junginger and Trauth, 2013).

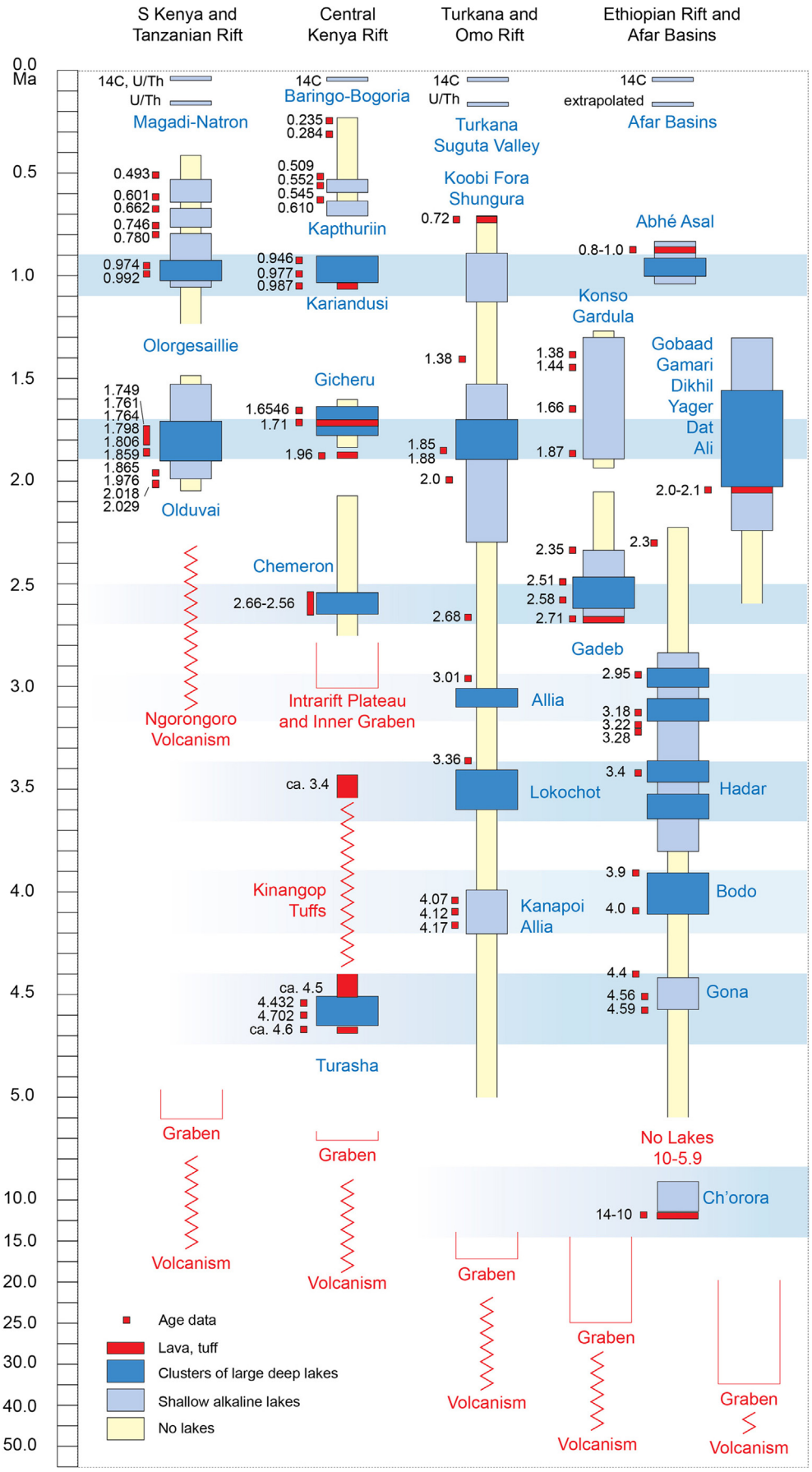

Fig. 3. Summary of the tectonic and lake occurrences in East Africa using data from Trauth et al. (2007); Maslin and Trauth (2009); Wichura et al. (2010, 2011); Underwood et al. (2013).

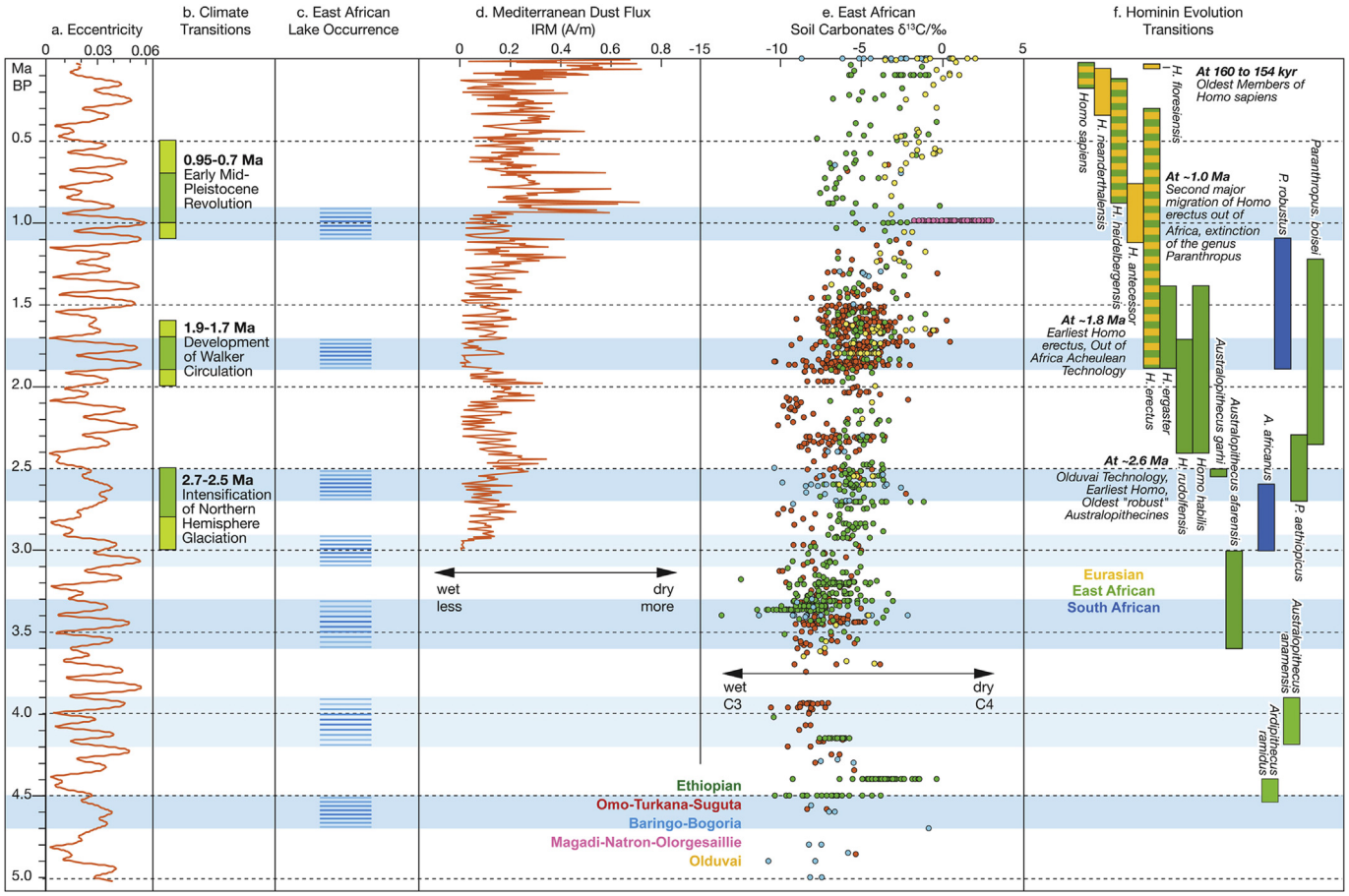

Fig. 4. Comparison of eccentricity variations (Berger and Loutre, 1991), East African lake occurrence (Trauth et al., 2005, 2007; Shultz and Maslin, 2013) with Mediterranean dust flux (Larrasoaña et al., 2003), soil carbonate carbon isotopes (Levin, 2013), with Hominin Evolution Transitions (see references in Shultz et al., 2012).

highly localised signal as it records vegetation on the northern coast of the Horn of Africa and is not representative of the EARS. The proposed aridity trend is also supported by climate model simulations (Sepulchre et al., 2006; Prömmel et al., 2013; Sommerfeld et al., in press). These studies demonstrate that as uplift increases, wind patterns became less zonal resulting in a decrease in regional rainfall. Hence as elevation increases, a rain shadow effect occurs that reduces moisture availability on the Rift Valley mountain side, producing the strong aridification trend evident in palaeoenvironmental records (Sepulchre et al., 2006; Prömmel et al., 2013). Maslin et al. (2012) also argue that East African soil carbonate carbon isotope records show increased aridity during the dry periods but that wet periods seem to remain at a similar level (Fig. 4). This suggests that the aridification trend in East Africa is instead a gradual progression towards a more variable climate with intensified arid periods.

In addition to contributing towards the aridification of East Africa, the tectonic activity described above also produced numerous basins suitable for lake formation (Trauth et al., 2010). Fig. 2 illustrates that tectonics was essential for the production of isolated basins in the East African Rift valley within which lakes can form. The southward propagation of rifting, including the formation of faults and magmatic activity, is also reflected in the earliest formation of lake basins in the northern parts of the rift (Fig. 3). For example, the Middle and Upper Miocene saw the beginning of lakes in the Afar, Omo-Turkana and Baringo-Bogoria Basins, but the oldest lacustrine sequences in the central and southern segments of the rift in Kenya and Tanzania are of Early Pliocene age (Tiercelin and Lezzar, 2002; Trauth et al., 2007). Palaeo-lakes in the northern part of the East African Rift Valley, thus formed earlier than in the South. However, if tectonics were the sole control over the appearance and disappearance of lakes, then either a N–S or NW–SE temporal pattern would be expected. In contrast, what is observed is the synchronous appearance of large deep lakes across a large geographical area at specific times (Trauth et al., 2005), possibly suggesting some other regional climatic control.

2.1. Limits to our current knowledge

There remain two main elements of regional tectonics in Africa that are not completely understood. First is the exact timing and altitude of the uplift. Much work has been done on the timing of key tectonic features, but uplift rates and maximum altitude are still unconstrained, especially for southern Africa. These factors control local rainfall patterns and thus are important for understanding the evolution of African climate. So although we know that progressive uplift and rifting has caused East Africa to dry, we do not know precisely when, or at what pace, these changes occurred (e.g., Forster and Gleadow, 1996; Spiegel et al., 2007; Pik et al., 2008; Wichura et al., 2010). The second factor is what effect tectonics had on vegetation. This is crucial for understanding hominin evolution. For example, at 10 Ma, while the doming of East Africa was occurring, how extensive were rainforests in East Africa (Couvreur et al., 2008)? When did the forest fragment? When did grasslands become important, and more specifically, dominant? Was there a vegetative corridor between southern Africa and

eastern Africa that may have facilitated dispersal and exchange between populations? At the moment we have detailed knowledge of vegetation and environmental conditions at sites containing hominin remains for East Africa and South Africa (e.g., Bonnefille, 1983, 2004, 2010; Kingston et al., 1994, 2007; Feakins et al., 2013; Barboni, 2014; Cerling, 2014). However, these only provide information on the niche that our ancestors inhabited and not the wider environment or regional climatic pattern. Moreover, many of these reconstructions are based on large sequences covering a wide range of time and may be affected by time-averaging (Hopley and Maslin, 2010), which means short-term, large scale variations in environment are grouped together. A very successful approach to these problems has been model reconstruction of climate and vegetation with greatly reduced relief over Eastern Africa (Sepulchre et al., 2006; Prömmel et al., 2013; Sommerfeld et al., in press). The next step would be to produce detailed time-slices through the last 8 million years with both relief and global climate applied to a regional climate and vegetation model.

3. East African rift system lakes

The sedimentary record of East Africa is rich in lake deposits (e.g., Gasse, 2000; Tiercelin and Lezzar, 2002; Barker et al., 2004; Trauth et al., 2005). This is because the southward propagation of rifting created lake basins along the entire length of the rift valley. A compiled record of lake occurrence was collated using the initial work of Trauth et al. (2005, 2007) and updated by Shultz and Maslin (2013). The collation is based on published geological evidence for the appearance of either deep ephemeral or shallow alkaline lakes in seven major basins in 50 kyrs sections over the last 5 Myrs (Tiercelin and Lezzar, 2002; Trauth et al., 2005, 2007, 2010; Deino et al., 2006; Kingston et al., 2007; Lepre et al., 2007; Joordens et al., 2011; McDougall et al., 2012; Feibel, 2011 and pers. comm.). These Basins, shown in Fig. 2, are: Olduvai (Tanzania), Magadi-Natron-Olorgesailie (N. Tanzania and S. Kenya), Central Kenya Rift (Kenya), Baringo-Bogoria (Kenya), Omo-Turkana-Suguta (N. Kenya), Ethiopian Rift (South and Central Ethiopia) and Afar (N. Ethiopia). The following indicators, as defined by Trauth et al. (2007), were used for large and deep freshwater palaeolakes: 1) the presence of pure white and frequently laminated diatomite, 2) typical freshwater diatom assemblages, and 3) a diatom flora clearly dominated by planktonic species, whereas benthic or epiphytic taxa are less frequent or absent. Shallow and more alkaline lake were defined by: 1) a significant clastic component in the diatomites, 2) diatom indicators for higher alkaline conditions, and 3) a significant benthic-epiphytic diatom community and the presence of abundant phytoliths and sponge spicules. Based on these characteristics, it is possible to classify the palaeoenvironments in the lake basins (Fig. 3). A deep freshwater lake, characterised by a size of several 100 km^2, water depths in excess of 150 m, and a neutral pH, is documented by pure white and frequently laminated diatomites, and planktonic/littoral diatom ratios reaching 10 and 100. In contrast, shallow and more alkaline lakes are typically less than 150 km^2 in size, have water depths much less than 100 m (often only a few metres), and dry out episodically. The pH of these lakes is often at around 8, but may reach significantly higher values. The corresponding sediments are clayey diatomites and silts, containing a diatom flora with planktonic/littoral diatom ratios of less than 1 (typically between 0.1 and 0.3 and, in some cases, up to 0.8). In extreme cases, the sediments contain authigenic silicates, such as zeolites, that document chemical weathering of silicic volcanic glass in an extremely alkaline lake environment. No lake, however, indicates the complete absence of lake sediments. Age control for the lake periods was obtained by published radiometric age determinations usually of anorthoclase and sanidine phenocryst concentrates from several tuff beds and lava flows. This compilation suggests that there were significant late Cenozoic lake periods between 4.6 and 4.4 Ma, 4.0–3.9 Ma, 3.6–3.3 Ma, 3.1–2.9 Ma, 2.7–2.5 Ma, 2.0–1.7 Ma, 1.1–0.9 Ma and 0.2–0 Ma before present in East Africa (Fig. 3). These occurrences correlate with the 400- and 800-kyrs components of the eccentricity cycle, suggesting a major role in lake formation for extreme amplitude fluctuations in precession (Fig. 4).

On very long time scales of 100,000s years, changes in lakes are primarily determined by tectonics, which initially creates but also destroys lake basins. However, tectonics also affects conditions in a lake over shorter time scales, such as through changes to the shape and size of catchments and drainage networks (e.g. Bergner et al., 2009; Olaka et al., 2010; Trauth et al., 2010; Feibel, 2011). Furthermore, tectonics shapes the morphology of lake basins and hence contributes to the sensitivity of these lakes to changes in the precipitation/evaporation balance (Olaka et al., 2010; Trauth et al., 2010). In the EARS many of the lake basin have become very sensitive to small changes in rainfall and are referred to as amplifier lakes (Trauth et al., 2010). These amplifier lakes are very sensitive to moderate climate change. For example, the water level of the Early Holocene palaeo-Lake Suguta rose to 300 m during a +25% change in precipitation during the African Humid Period (ca 15,000–5000 yr BP) (Garcin et al., 2009; Borchardt and Trauth, 2011; Junginger and Trauth, 2013; Junginger et al., 2014). On the other hand, as hydrological modelling suggests, large water bodies buffer rapid shifts in climate due to their delayed response to changes in the precipitation-evaporation balance (Borchardt and Trauth, 2012). Thus theoretically, lakes can be very quick to form but their effect on the local climate will create an inertia resisting its removal or disappearance.

3.1. Limits to our current knowledge

The identification and correlation of episodes of deep and shallow lake occurrence between lake basins is unfortunately hampered by ambiguous interpretation of environmental indicators or proxies within the sediments (Owen et al., 2008, 2009; Trauth and Maslin, 2009). Moreover, the fragmented nature of the lake sediments can give rise to highly localised interpretations of environmental variations. Thus, the compilation of all published data has been used to provide a regional overview of lake occurrence to mitigate against the local influences of a region for which the landscape becomes more heterogeneous over time. Furthermore, fluctuating sedimentation rates and hiatuses between radiometric age dates, which themselves contain errors, complicate the assessment of the actual timing of environmental changes (e.g., Blaauw, 2010; Schumer et al., 2011; Trauth, 2014). Standardised terminology and interpretation of sedimentology between the key sites is required and new statistical methods are needed to model hiatuses and lake sediment occurrence between dispersed age controls (Trauth, 2014).

4. Late Cenozoic global climate transitions

During the period of early human evolution in Africa there are five major transitions or climate events that would have influenced African climate: 1) the emergence and expansion of C_4 dominated biomes (~8 Ma onwards), 2) the Messinian Salinity Crisis (6–5.3 Ma), 3) the intensification of Northern Hemisphere Glaciation (iNHG, 3.2–2.5 Ma), 4) the development of the Walker Circulation (DWC, 2.0–1.7 Ma), and 5) the Early–Middle Pleistocene Transition (EMPT, 1.2–0.8 Ma).

The emergence and expansion of C_4 grass-dominated biomes which took place during the Mid to Late Miocene (Edwards et al.,

2010; Brown et al., 2011), is thought to have been driven by lower atmospheric carbon dioxide. This is a global climate event as C_4 grass-dominated biomes had long-lasting impacts on continental biota; including major shifts in vegetation structure, characterised in Africa by shrinking forests and the emergence of more open landscapes accompanied by large-scale evolutionary shifts in faunal communities. A threshold in carbon dioxide concentrations was breached at ~30 Ma, leading to the development of the C_4 photosynthetic pathway (Tipple and Pagani, 2007). Ségalen et al. (2007) dispute this early emergence and suggest, from paedogenic and biogenic carbonate $\delta^{13}C$ data, that evidence for C_4 plants before ~8 Ma is weak. These contrasting views suggest differing patterns of environmental change and their links to faunal shifts, including those of early hominins. There is clear, undisputed evidence for the emergence of substantial C_4 biomass from 7 to 8 Ma (Cerling, 2014) while C_4 plants appeared later in mid-latitude sites.

The second regional climate event is the Messinian Salinity Crisis. The tectonic closure of the Strait of Gibraltar led to the transient isolation of the Mediterranean Sea from the Atlantic Ocean. During this isolation the Mediterranean Sea desiccated several times, resulting in vast evaporite deposits. This Messinian Salinity Crisis removed nearly 6% of all dissolved salts in the oceans, changing the alkalinity. The onset of the Messinian Salinity Crisis at 5.96 ± 0.02 Ma while full isolation occurred at 5.59 Ma (Krijgsman et al., 1999; Roveri et al., 2008, in press 2014). Normal marine conditions were re-established with the Terminal Messinian Flood at 5.33 Ma (Bickert et al., 2004) and a significant amount of salt was returned to the world's oceans via the Mediterranean-Atlantic gateway. At present, little is known concerning the effect of the Messinian Salinity Crisis on Northern and East African climate. Climate modelling studies indicate that there was no impact in Southern Africa with only weak precipitation changes in East Africa (Murphy et al., 2009; Schneck et al., 2010). The spectral resolution of the existing studies may lead to uncertainties in their representation of African topography (Schneck et al., 2010) and further work is needed (Roveri et al., in press 2014).

The intensification of Northern Hemisphere Glaciation (iNHG) was the culmination of long-term high latitude cooling, which began with the Late Miocene glaciation of Greenland and the Arctic, and continued through to the major increases in global ice volume around 2.55 Ma (Li et al., 1998; Maslin et al., 1998). This intensification of Northern Hemisphere glaciation seems to have occurred in three key stages: a) the Eurasian Arctic and Northeast Asia were glaciated at c. 2.75 Ma, b) glaciation of Alaska at 2.70 Ma, and c) the significant glaciation of the North East American continent at 2.54 Ma (Maslin et al., 2001). The extent of glaciation did not evolve smoothly after this, but instead was characterised by periodic advances and retreats of ice sheets on a hemispherical scale – the 'glacial-interglacial cycles'. Various causes of the iNHG have been postulated including the uplift and erosion of the Tibetan-Himalayan plateau (Ruddiman and Raymo, 1988; Raymo, 1991, 1994), the deepening of the Bering Straits (Einarsson et al., 1967) and/or the Greenland–Scotland ridge (Wright and Miller, 1996), the restriction of the Indonesian seaway (Cane and Molnar, 2001), and the emergence of the Panama Isthmus (Keigwin, 1978, 1982; Keller et al., 1989; Mann and Corrigan, 1990; Haug and Tiedemann, 1998). It is also possible that there was no trigger, but that the long-term decrease in atmospheric CO_2 (Fedorov et al., 2013) passed a critical threshold (Crowley and Hyde, 2008; DeConto et al., 2008; Abe-Ouchi et al., 2013).

In terms of the tropics and particularly Africa, there is evidence for a more extreme climate from 2.7 Ma onwards. deMenocal (1995, 2004) suggests there was significant increase in the amount of dust coming off the Sahara and Arabia, indicating aridity in the region in response to the iNHG; though this has been disputed by Trauth et al. (2009). Meanwhile, there is also evidence for the growth and decline of large lakes between 2.7 and 2.5 Ma in the Baringo–Bogoria Basin (Deino et al., 2006; Kingston et al., 2007) and on the eastern shoulder of the Ethiopian Rift and in the Afar Basin (Williams et al., 1979; Bonnefille, 1983). The presence of large, ephemeral lakes such as these is indicative of a highly variable and changing climatic regime.

Until recently, the iNHG and the EMPT were the only two major climate changes recognized in the last 5 million years. This is because in terms of global ice volume very little happens between 2.5 Ma and 1 Ma: glacial–interglacial cycles occur roughly every 41 kyrs and are of a similar magnitude (Lisiecki and Raymo, 2005). However, a clear shift in long-term records of sea surface temperature (SST) in the Pacific Ocean is evident at 1.9–1.6 Ma (Ravelo et al., 2004; McClymont and Rosell-Melé, 2005; Brierley et al., 2010), when a strong east–west temperature gradient developed across the tropical Pacific Ocean. This change was also matched by a significant increase in seasonal upwelling off California (Liu et al., 2008). Ravelo et al. (2004) suggest this is evidence for the development of a stronger Walker circulation (DWC), as strong easterly Trade winds are required to set up the enhanced E–W SST gradients. They suggest this switch was part of the gradual global cooling and at about 2 Ma the tropics and sub-tropics switched to the modern mode of circulation with relatively strong Walker circulation and cool sub-tropical temperatures. Alternate proxy records of the equatorial SST gradient do not lead to as distinct a transition (Fedorov et al., 2013), yet a change in the Walker circulation about 1.9 Ma coincides with numerous changes in the tropics. For example, Lee-Thorp et al. (2007) use $^{13}C/^{12}C$ ratios from fossil mammals to suggest that although there was a general trend towards more open environments after 3 Ma, the most significant environmental change to open, grassy landscapes occurred after 2 Ma rather than 2.4–2.6 Ma as earlier suggested. The re-analysis of terrestrial dust records from the Arabian Sea (deMenocal, 1995, 2004), the eastern Mediterranean Sea (Larrasoaña et al., 2003) and off subtropical West Africa (Tiedemann et al., 1994) using a breakfit regression analysis method suggests an increase in aridity and variability on the continent after ~1.9–1.5, which coincides with the DWC (Trauth et al., 2009). At about the same time, there is also evidence for large deep, but fluctuating lakes occurring in East Africa (Trauth et al., 2005, 2007; Fig. 4.7). The DWC provided another interesting twist on African climate: it is thought that a strong east-west temperature gradient in the Pacific Ocean impacts upon the properties of the El Niño-South Oscillation (ENSO) and, as a consequence of that, the Indian Ocean Dipole (IOD) as the main cause of interannual variability in rainfall in the region today (e.g., Saji et al., 1999). Hence we need to understand how changes in interannual variability may have influenced East Africa and how it changed through the Plio-Pleistocene.

The Early–Middle Pleistocene transition (which was previously known as the Mid-Pleistocene Transition or Revolution; Head et al., 2008) is the marked prolongation and intensification of glacial-interglacial climate cycles initiated sometime between 900 and 650 Ka (Mudelsee and Stattegger, 1997). Before the EMPT, global climate conditions appear to have responded primarily to the obliquity orbital periodicity (Imbrie et al., 1992). The consequences of this are glacial-interglacial cycles with a mean period of 41 kyrs. After about 800 Ka, glacial–interglacial cycles occur with a much longer mean quasi-periodicity of ~100 kyrs, with a marked increase in the amplitude of global ice volume variations. The ice volume increase may in part be attributed to the prolonging of glacial periods and thus of ice accumulation (Prell, 1984; Shackleton et al., 1988; Berger and Jansen, 1994; Tiedemann et al., 1994; Mudelsee and Stattegger, 1997; Abe-Ouchi et al., 2013). The amplitude of ice volume variation may also have been impacted by the extreme

warmth of many of the post- EMPT interglacial periods; similar interglacial conditions can only be found at ~1.1 Ma, ~1.3 Ma and before ~2.2 Ma. The EMPT, in addition to marking a change in periodicity, also marks a dramatic sharpening of the contrast between warm and cold periods. Mudelsee and Stattegger (1997) used time-series analysis to review deep-sea evidence spanning the EMPT and summarised the salient features. They suggest that the EMPT was actually a two-step process with the first transition between 940 and 890 Ka, when there is a significant increase in global ice volume, and the dominance of a 41 kyrs climate response. This situation persists until the second step, at about 650–725 Ka, when the climate system finds a three-state solution and strong 100 kyrs climate cycles begin (Mudelsee and Stattegger, 1997). These three states have more recent analogues and correspond to: 1) full interglacial conditions, 2) the mild glacial conditions characteristic of Marine (oxygen) Isotope Stage (MIS) 3 and 3) maximum glacial conditions characteristic of MIS 2 (i.e., the Last Glacial Maximum (LGM) (Maslin and Ridgwell, 2005). The EMPT had a significant effect on African climate. Ségalen et al. (2007) concluded that C_4 grasses remained a relatively minor component of African environments until the late Pliocene and early Pleistocene. Paedogenic carbonate $d^{13}C$ data from existing localities in East Africa suggest that open ecosystems dominated by C_4-grass components emerged only during the EMPT (i.e., after ~1 Ma). There is also evidence that the EMPT may have lead to the formation of large ephemeral lakes between 1.1 and 0.9 Ma in East Africa e.g., Olorgesailie Formation, the Naivasha and Elmenteita–Nakuru basins, and the Afar Basin (Trauth et al., 2005, 2007).

4.1. Limits to our current knowledge

The major difficulty in understanding the effects of these global climate transitions on African climate is the lack of high-resolution continental records. This problem is particularly acute for southern Africa. The terrestrial realm is severely restricted in the types of proxies that can be utilised, as well as the ability to accurately constrain the ages of the sediments, since in many cases the original record is removed through processes associated with subaerial exposure (e.g., Lowe and Walker, 1984). The continental records that have been published generally do not provide the same level of continuous, detailed climate information as ocean records. Most of these continental records have a resolution greater than 10 kyrs, which may cause the problem of climate-averaging (Hopley and Maslin, 2010), whereby sediment and fauna from two very different climate regimes (say, two precession-scale periods) are lumped together. This means that many of the hominin habitat reconstructions may be incorrect as they combine two very different climates and thus vegetation cover in one signal (Hopley and Maslin, 2010). Individuals would only experience one of the climates rather than the average one.

At present, in the terrestrial realm, only lakes and caves provide relatively continuous records. Lakes sediments are present throughout East Africa and the long-core drilling program at Lake Malawi has recovered a continuous sediment core record spanning the last 145 ka (Scholz et al., 2011, and references therein). Caves are present in southern Africa, and whilst the cave deposits have yielded abundant specimens, the stratigraphy of the caves is often highly complex (e.g., Scott, 1999). Most of these sites were quarried first and analysed later, thus severely impacting stratigraphic control. Finally, where there is limited stratigraphic control, records are sometimes dated based on an assumption of cause/association with global events rather than on an independent chronology. For example, the evidence for increased aridity associated with the iNHG was derived, as outlined in Partridge (1993), from geomorphological and biostratigraphic datasets that are not independent from one another and like many longer-term palaeoclimate records cannot be dated with precision.

5. Influence of orbital forcing on African climate

Orbital forcing has an obvious impact on high latitude climates and influenced late Cenozoic global climate transitions, but it also has a huge influence in the tropics, particularly through precession and its effect on seasonality and thus rainfall. There is a growing body of evidence for precession-forcing of moisture availability in the tropics, both in East Africa during the Pliocene (deMenocal, 1995, 2004; Trauth et al., 2003; Denison et al., 2005; Deino et al., 2006; Hopley et al., 2007; Kingston et al., 2007; Lepre et al., 2007; Wilson, 2011; Magill et al., 2013; Ashley et al., 2014) and elsewhere in the tropics during the Pleistocene (Bush et al., 2002; Clemens and Prell, 2003, 2007; Trauth et al., 2003; Wang et al., 2004; Cruz et al., 2005; Tierney et al., 2008; Verschuren et al., 2009; Ziegler et al., 2010). The precessional control on tropical moisture has also been clearly illustrated by climate modelling (Clement et al., 2004) which showed that an 180° shift in precession could change annual precipitation in the tropics by at least 180 mm/year and cause a significant shift in seasonality. This is on the same order of magnitude as the effect of a glacial–interglacial cycle in terms of the hydrological cycle. In contrast, precession has almost no influence on global or regional temperatures. Support for increased seasonality during these periods of climate variability also comes from mammalian community structures (Reed, 1997; Bobe and Eck, 2001; Reed and Fish, 2005) and hominin palaeodiet reconstructions (Teaford and Ungar, 2000).

In northern and eastern Africa there are excellent records of precessional-forcing of climate including: 1) East Mediterranean marine dust abundance (Larrasoaña et al., 2003), which reflects the aridity of the eastern Algerian, Libyan, and western Egyptian lowlands located north of the central Saharan watershed, 2) sapropel formation in the Mediterranean Sea, which is thought to be caused by increased Nile River discharge (Lourens et al., 2004; Larrasoaña et al., 2013), and 3) dust records from ocean sediment cores adjacent to West Africa and Arabia (deMenocal, 1995, 2004; Clemens and Prell, 2003, 2007; Ziegler et al., 2010). There is also a growing body of evidence for precessional forcing of East African lakes. Deino et al. (2006) and Kingston et al. (2007) have found that the major lacustrine episode of the Baringo Basin in the Central Kenyan Rift between 2.7 and 2.55 Ma actually consisted of five palaeo-lake phases separated by a precessional cyclicity of ~23 kyrs. While Magill et al. (2013) have found biomarker stable carbon isotope evidence in Olduvai lake sediment of precessional forced variations between open C_4 grasslands and C_3 forest between 1.8 and 1.9 Ma. There is also evidence for precessional forcing of the 1.9–1.7 Ma lake phase indentified in the KBS Member of the Koobi Fora Formation in the northeast Turkana Basin in Kenya (Brown and Feibel, 1991; Lepre et al., 2007). Precessional forcing of vegetation change also occurred at this time in Southwest Africa, independent of glacial-interglacial cycles (Denison et al., 2005). 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 (Hopley et al., 2007). The occurrences of these environmental changes are in-phase with increased freshwater discharge and thus sapropel formation in the Mediterranean Sea (Lourens et al., 2004; Larrasoaña et al., 2013), and coincide with dust transport minima recorded in sediments from the Arabian Sea (deMenocal, 1995, 2004; Clemens et al., 1996). Hence, the lake records from East Africa and the Arabian Sea dust records document extreme climate variability with precessionally-forced wet and dry phases.

Table 2
Late Pliocene – early Pleistocene compilation of published pan-East African palaeo-records that contain evidence of precessional forcing of the local environment.

Location	Date range (Ma)	Number of precessional cycles	Evidence for millennial scale variability	Proxy data	References
East Africa					
Turkana Basin (Koobi Fora Ridge)	~1.9–1.6 Ma	6 (authors suggest it could also be obliquity)	No	Lithology	Brown and Feibel (1991), Lepre et al. (2007)
Turkana Basin (Karari Ridge: upper Burgi Member)	1.960–1.835	5.5	No	Lithology and Sr isotopes	Joordens et al. (2011)
Baringo Basin	2.7–2.55	5	Yes	Lithology and diatom oxygen isotopes	Deino et al. (2006), Kingston et al. (2007), Wilson (2011), Wilson et al. (submitted)
Olorgesailie basin	1.1 and 0.9	(authors suggest precessional cycles but not how many)	Yes	Lithology	Potts et al. (1999, 2013), Owen et al. (2008)
Olduvai Gorge	1.85–1.74	5.5	No	Lithology and biomarker carbon isotopes	Ashley (2007), Ashley et al. (2014), Magill et al. (2012, 2013)
North Africa					
East Mediterranean	3.00–0	~130	No	Dust records	Larrasoaña et al. (2003)
East Mediterranean	5.35–0	~150	No	Sapropels	Lourens et al. (2004), Larrasoaña et al. (2013)
Indian Ocean region					
Arabian Sea	3.00–0	~130		Dust records	Clemens and Prell (2003, 2007), deMenocal (1995; 2004
South Africa					
Buffalo Cave flowstone	2.00–1.52	~21		Oxygen isotope	Hopley et al. (2007)

Although the direct influence of orbital forcing on African climate seems straightforward, isolating the driving forces is extremely complex. It is clear that high-latitude orbital forcing influences glacial-interglacial cycles, which in turn seems to have an increasing influence on African climate through the Pleistocene. The main effects are: 1) Pole-Equator temperature gradients, 2) sea surface temperatures (SST's), 3) wind strength and direction, and 4) atmospheric carbon dioxide, methane and water vapour content. Studies of late Quaternary palaeovegetation records indicate that equatorial African ecosystems are highly sensitive to glacial-interglacial cycles, and that these are associated with atmospheric CO_2 changes and regional temperature changes, resulting in rapid shifts in pollen assemblage indices (Lezine, 1991; Bonnefille and Mohammed, 1994; Elenga et al., 1994), charcoal fluxes (Verardo and Ruddiman, 1996), and relative proportions of C_3 (trees, shrubs, cold-season grasses and sedges) and C_4 (warm-season grasses and sedges) biomarkers (Huang et al., 1999; Ficken et al., 2002; Schefuß et al., 2005). There is also the combined effect of high and low latitude orbital forcing which must be considered. After the EMPT we can consider four 'climate phases': 1) glacial with positive precession, 2) glacial with negative precession; 3) interglacial with positive precession; and 4) interglacial with negative precession (Maslin et al., 2005). All of these phases/periods have a distinct effect on the moisture, temperature and greenhouse gas content of the atmosphere. An additional complication has been proposed by Berger et al. (2006). During any year in the tropics, there are two insolation maxima when the sun is over the Equator (spring and autumn equinoxes), and two insolation minima when the sun is over the Tropic of Cancer and Capricorn (summer and winter solstice). The magnitude of the maxima and minima, thus insolation at equinox and solstice, are controlled by precession. Berger et al. (2006) has calculated the maximum insolation year and shown that it peaks every ~11.5 kyrs. This is because as the spring equinox's insolation maximum is reduced, the autumnal equinox's insolation maximum is increased. Berger et al. (2006) calculated the maximum seasonality, defined as the difference between the maximum and minimum solar insolation in any one year, and found a cyclic seasonality of 5 kyrs. Climate in tropical Africa could, therefore, respond to orbital forcing of seasonality at both 11.5 kyrs and 5 kyrs intervals. Evidence for this half precession forcing of East Africa climate has been found in lake sediments by Trauth et al. (2003) and Verschuren et al. (2009).

5.1. Limits to our current knowledge

We are only just starting to understand the complex relationship between orbital forcing and African climate. This complexity is in part due to the fact that much of tropical Africa is influenced by high latitude orbitally-forced climate changes and thresholds as well as local, direct orbital forcing, which is dominated by precession. Table 2 shows the preliminary evidence that supports a precessional (23 kyrs) control on moisture availability in East Africa (Clemens and Prell, 2003, 2007; Deino et al., 2006; Kingston et al., 2007; Ashley, 2007; Wilson, 2011, 2013; Ashley et al., 2014), South Africa (Partridge, 1993, 1997; Hopley et al., 2007), southwest Africa (Denison et al., 2005) and North Africa and the Mediterranean (Larrasoaña et al., 2003, 2013; Lourens et al., 2004). The fundamental question is whether the precessional forcing of local climate at these particular sites can be extrapolated and applied to the whole of East Africa and beyond. Only by accumulating more data from key palaeo-lake sites will it be possible to definitely answer this question. In addition to this, more evidence is required to better understand the role of climate forcing at half- and quarter-precessional periods, and its effect on seasonality in the tropics.

6. Early human evolution

The fossil record suggests four main stages in hominin evolution: 1) the appearance of the earliest (proto) hominins attributed to the genera *Sahelanthropus*, *Orronin* and *Ardipithecus* between four and seven million years ago, 2) the appearance of the *Australopithecus* genus around four million years ago and the appearance of the robust *Paranthropus* genus around 2.7 Ma, 3) the appearance of the genus *Homo* around the Plio-Pleistocene boundary between 1.8 and 2.5 Ma and 4) the appearance of anatomically modern humans around 200 ka. The taxonomic classification of many specimens, as well as their role in the evolution of modern humans is continually discussed (e.g., Lordkipanidze et al., 2013). What is not disputed is that, apart from *Sahelanthropus* remains from Chad, all the earliest specimens for

each of the main genera were found in the East African Rift System. Thus, although the World Heritage site, the Cradle of Humankind, is in South Africa, the available evidence currently suggests that all of the major stages in human evolution (at 7 Ma, 4 Ma, 2 Ma, and 200 ka) occurred in the East Africa (Wood, 2014).

The earliest disputed hominin is *Sahelanthropus chadensis*, dated to approximately seven million years ago (Brunet et al., 2002; Wood, 2002). The remains are limited to cranial fragments that suggest a mosaic of hominin and non-hominin features and a brain size equivalent to modern chimpanzees (Guy et al., 2005). The lack of post-cranial remains makes it extremely difficult to reconstruct its lifestyle and whether it was bipedal or whether it was truly a hominin. The next putative hominin is *Orronin tungenesis* from Western Kenyan deposits aged around 6 Ma (Senut et al., 2001) but its taxonomic position, lifestyle and locomotion are all disputed due to the fragmentary nature of the specimens. Both *Sahelanthropus* and *Orronin* have been suggested to be members of a clade that includes *Ardipithecus* (Guy et al., 2005). The oldest member of the *Ardipithecus* genus is *Australopithecus kadabba*, whose fossil evidence consists only of fragmentary teeth and skeletal remains dated to approximately 5.5 Ma (Haile-Selassie et al., 2004). A much more extensive fossil record exists for the second member of the genus, *Ardipithecus ramidus*. *Ardipithecus* had brain and body sizes roughly equivalent to modern chimpanzees, their teeth indicate a highly omnivorous diet and their post-crania suggest a lifestyle of arboreality coupled with primitive bipedality (White et al., 2009). The fauna and vegetation associated with the *A. ramidus* specimens in the Awash valley dating to around 4.4 Ma suggest a woodland–forest matrix habitats, associated with significant rainfall and water availability (White et al., 2009; Cerling et al., 2010; Cerling, 2014). This appearance of bipedality in closed woodland environments undermines theories of bipedality evolving as an adaptation to open habitats.

The first members of the *Australopithecus* genus, attributed to *Australopithecus anamensis*, appeared around four million years ago (Leakey et al., 1995). These individuals show strong evidence of bipedality combined with primitive cranial features. They are followed by *Australopithecus afarensis*, which is very well known from the fossil record and includes the remarkably complete 'Lucy' specimen. *Afarensis* still retains a small brain size, yet the post-cranial morphology is very similar to modern humans and suggests a lifestyle strongly adapted to long-distance walking (Stern and Susman, 1983). *Australopithecus africanus*, the first hominin found in South Africa, is similar to *A. afarensis* but with more ape-like limb proportions yet less primitive teeth (Green et al., 1997). The final gracile australopithecine is *A. anamensis*, associated with 2.5 Ma old deposits in the Awash Valley, Ethiopia. It is characterised by a longer femur than the other Australopithecines, suggesting longer strides and more efficient walking style (Green et al., 1997). In a separate development, a group of hominins with robust dentition and jaw muscles appeared around 2.5 Ma. These hominins, generally attributed to the *Paranthropus* genus, include the East African *Paranthopus aethiopicus* (2.5 Ma) and *Paranthopus bosiei* (2.3–1.2 Ma) and the Southern African *Paranthopus robustus* (1.8–1.2 Ma). Who have been attributed to more open habitats (Cerling, 2014), though the evidence to support this inference has been questioned (Wood and Strait, 2004).

The first fossil evidence of *Homo* comes from 1.8 to 1.9 million year old EARS deposits. *Homo habilis* had a gracile morphology similar to the australopithecines (Wood, 2014), and a brain size only slightly larger, leading to some arguing it should not be classified as *Homo* (Collard and Wood, 2007). *H. habilis* was then followed by the appearance of *Homo erectus sensu lato*, which is associated with sweeping changes in brain size, life history, and body size and shape. Post-cranially, *H. erectus* is very similar to anatomically modern humans. Inferences from fossil demography are that development slowed down, coupled with decreased inter-birth. The final stages in the evolution of modern humans were the appearance of *Homo heidelbergensis* around 800 ka and anatomically modern humans around 200 ka.

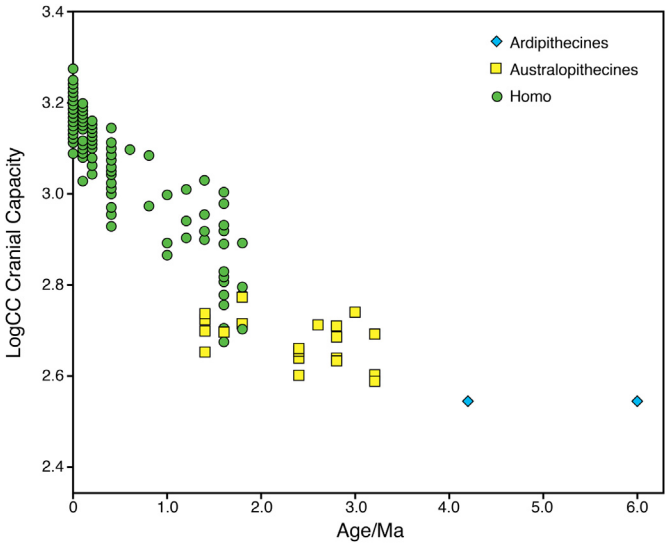

Fig. 5. Comparison of the log of hominin brain capacity for fossils covering the last 6 million years (data from Shultz et al., 2012 updated in Shultz and Maslin, 2013).

Arguably the most important episode in hominin evolution occurred in East Africa around 1.8–1.9 Ma when hominin diversity reached its highest level with the appearance of the robust *Paranthropus* species, as well as the first specimens attributed to genus *Homo* (*sensu stricto*). In addition to speciation, a second major process that begins during this period is the episodic migration of hominins out of the Rift Valley and into Eurasia. This period also witnessed the most dramatic increases in hominin brain size; early representatives of the *H. erectus sensu lato* (*H. erectus* and *Homo ergaster*) in Africa had a brain that was >80% larger than the gracile australopithecine *A. afarensis* and ~40% larger than *Homo* (*Australopithecus*) *habilis* (Fig. 5). In contrast, from the appearance of the early australopithecines until the appearance of the first member of the genus *Homo*, there was remarkably little change in hominin brain size.

The emergence of the *H. erectus sensu lato* in East Africa represents a fundamental turning point in hominin evolution. Not only was there a dramatic increase in brain size, but also in life history (shortened inter-birth intervals, delayed development), body size, shoulder morphology allowing throwing of projectiles (Roach et al., 2013), adaptation to long distance running (Bramble and Lieberman, 2004), ecological flexibility (Hopf et al., 1993) and social behaviour (Antón, 2003). Some of these changes are consistent with a change in strategy towards flexibility and the ability to colonise novel environments. In contrast, the robust *Australopithecus sp.* adopted specialised habitat and dietary strategies (Reed, 1997; Reed and Russak, 2009). Thus, two strategies arose during this period, one of increased flexibility and one of increased specialisation. With the appearance of *H. erectus*, brain size increased significantly and continued to increase over the following 500 kyrs, followed by additional step increases between 0.8 and 1 Ma, at 200 ka and finally again at 100 ka (Shultz et al., 2012, Fig. 5). These final stages of increased brain capacity were due to the appearance of *H. heidelbergensis* around 800 ka and anatomically modern humans around 200 ka.

6.1. Limits to our current knowledge

The recent expansion of the hominin fossil record has been dramatic, with eleven new species and four new genera named since 1987. This richer fossil record has provided two major improvements. Firstly, this has led to a much greater understanding of the range of variation in the hominin phenotype, including in 'real' biological populations with evidence from Atapuerca, Dmanisi, and Hadar. Secondly, extensive use of new dating techniques has provided chronological precision to link those phenotypes to the environments in which they evolved. However the fossil record is still very limited with many gaps, the most significant for this study is the lack of cranial capacity data between 2 Ma and 2.5 Ma. There are also considerable discussions about defining the new species and genera (Lordkipanidze et al., 2013), which has an influence on the diversity curves presented in Fig. 6. However, conflating or expanding the defined species has little overall influence on the diversity pattern as it is clear when new species emerge but not necessarily how many. The other key debate is where all the new hominin species evolved. The fossil record at the moment suggests that the majority of the new species evolved in East Africa and then dispersed outwards. This is supported by the current brain capacity evidence, which suggests brain expansion occurs first in East Africa and only appears elsewhere once there has been a dispersal event. However it should be noted that other authors suggest South Africa, European and Asian origins for hominin speciation.

7. Linking African palaeoclimate with early human evolution

The relationship between climate and human evolution seems intuitive and indeed environmental factors have been suggested as a driving force in hominin evolution by many authors (See Kingston, 2007, for detailed history). Vrba (1985) first identified global climate change as a cause of African mammalian evolution by documenting radiations in bovid species at ~2.5 Ma coincident with the iNHG, which led to the development of the *turnover pulse hypothesis*. However, with greater knowledge of African palaeoclimates and mammalian fossil records, the timing if not the underlying mechanisms have been questioned. When the *turnover pulse hypothesis* was first developed, the field of palaeoclimatology was in its infancy, and through subsequent scientific ocean drilling it has become clear that 1) the iNHG was a long-term intensification beginning much earlier than 2.5 Ma (Tiedemann et al., 1989), and 2) connections between high latitudes and low to middle latitudes are not as straightforward as originally thought. The concept that significant global climate change forced major evolutionary changes in hominins remains pertinent, but both the idea of a turnover and the timing of such events have changed. It seems that iNHG had less of an impact on the region (e.g., Behrensmeyer et al., 1997; Faith and Behrensmeyer, 2013) than the development of Walker Circulation at ~1.8 Ma (Ravelo et al., 2004). With greater understanding of African palaeoclimates has also come new thinking about human evolution. The *variability selection hypothesis* (Potts, 1996, 1998, 2013) suggests that a long-term trend with an increasingly complex intersection of orbitally-forced changes in insolation and earth-intrinsic feedback mechanisms results in extreme, inconsistent environmental variability selecting for behavioural and morphological mechanisms that enhance adaptive variability. However currently we do not have evidence for increased variability of climate nor does it explain the pulsed nature of human evolution.

There is now evidence, presented above, of periods of extreme environmental variability during the Plio-Pleistocene (Trauth et al., 2005, 2007, 2010; Deino et al., 2006; Kingston et al., 2007; Maslin and Trauth, 2009; Magill et al., 2013; Potts, 2013; Ashley et al., 2014). These periods of extreme climate variability would have had a profound effect on the climate and vegetation of East Africa and, we suggest, human evolution. Hominin evolution in East Africa has distinct speciation events some of which are linked to increasing brain size. Figs. 5 and 6 show a new compilation of estimated cranial capacity (Shultz et al., 2012). Current available evidence suggests that hominin encephalisation is a combination of processes with an underlying gradual trend towards larger brains, punctuated by several large step increases at ~1.9 Ma and ~200 Ka (Fig. 5). By collating all available palaeoclimate data (e.g. the global benthic foraminifera $\delta^{18}O$ record, regional aeolian dust flux data and the East African lake record), Shultz and Maslin (2013) found that hominin speciation events and changes in brain size seem to be statistically linked to the occurrence of ephemeral deep-water lakes (Fig. 6). An example is the appearance of the *H. erectus sensu lato*, which is associated with the period of maximal ephemeral lake coverage (2 Ma). The expansion in cranial capacity occurs during one of only two periods when there is evidence for at least 5 of the 7 major intra-rift lake basins being active. Subsequently, the underlying trend towards increasing brain size in *Homo* is most strongly correlated with both decreases in lake presence and high levels of dust deposition in the Mediterranean record (Shultz and Maslin, 2013), indicating drier conditions in East Africa (Larrasoaña et al., 2003, 2013; Trauth et al., 2009). Shultz and Maslin (2013) suggested that large steps in brain expansion in East Africa may have been driven by climate variability while the smaller steps were due to regional aridity.

The periodic hominin dispersal events also seem to correlate with periods of high climate variability. It has been suggested that both lake presence and absence could be associated with these dispersal events (Trauth et al., 2010; Shultz and Maslin, 2013). For example, when the lake basins are dry they become 'hyper-arid' and thus uninhabitable and hence hominin populations would have been forced to migrate to the north and south (Trauth et al., 2010). However severe lack of resources would mean there was only a small and possibly shrinking population that could migrate. The absence of lakes may have facilitated allopatric speciation in key refugia such as Turkana, which may have remained wet. Dispersal is thus more likely to have occurred when the basins were completely filled with water, as there would have been limited space for the hominin populations on the tree covered Rift shoulders and river flood plains (Shultz and Maslin, 2013). The wet conditions could have been more conducive to dispersal because hominin populations could expand due to the availability of water and food and could follow the Nile tributaries northward and through a green Lavant region (Larrasoaña et al., 2013). So the occurrence of deep freshwater lakes would have forced expanding hominin populations both northwards and southwards generating a pumping effect pushing them out of East Africa towards the Ethiopian highlands and the Sinai Peninsula or into Southern Africa with each successive precessional cycle (Shultz and Maslin, 2013).

Fundamental to understanding which evolutionary mechanisms could have applied to hominins in East Africa are the speed and form of the transitions between lakes appearing and disappearing from the landscape. At first it may appear that orbitally-forced climatic oscillations may be too long-term to have significant effects on biota. However, this does not take account of the sinusoidal nature of orbital forcing or the threshold nature of the African lake systems. All orbital parameters are sinusoidal, which means that there are periods of little or no change followed by periods of large change. For example, the sinusoidal precessional forcing at the equator consists of periods of less than 2000 years during which 60% of total variation in daily insolation and seasonality occurs. These are followed by ~8000 years when relatively little change in daily insolation occurs (Maslin et al., 2005). Hence,

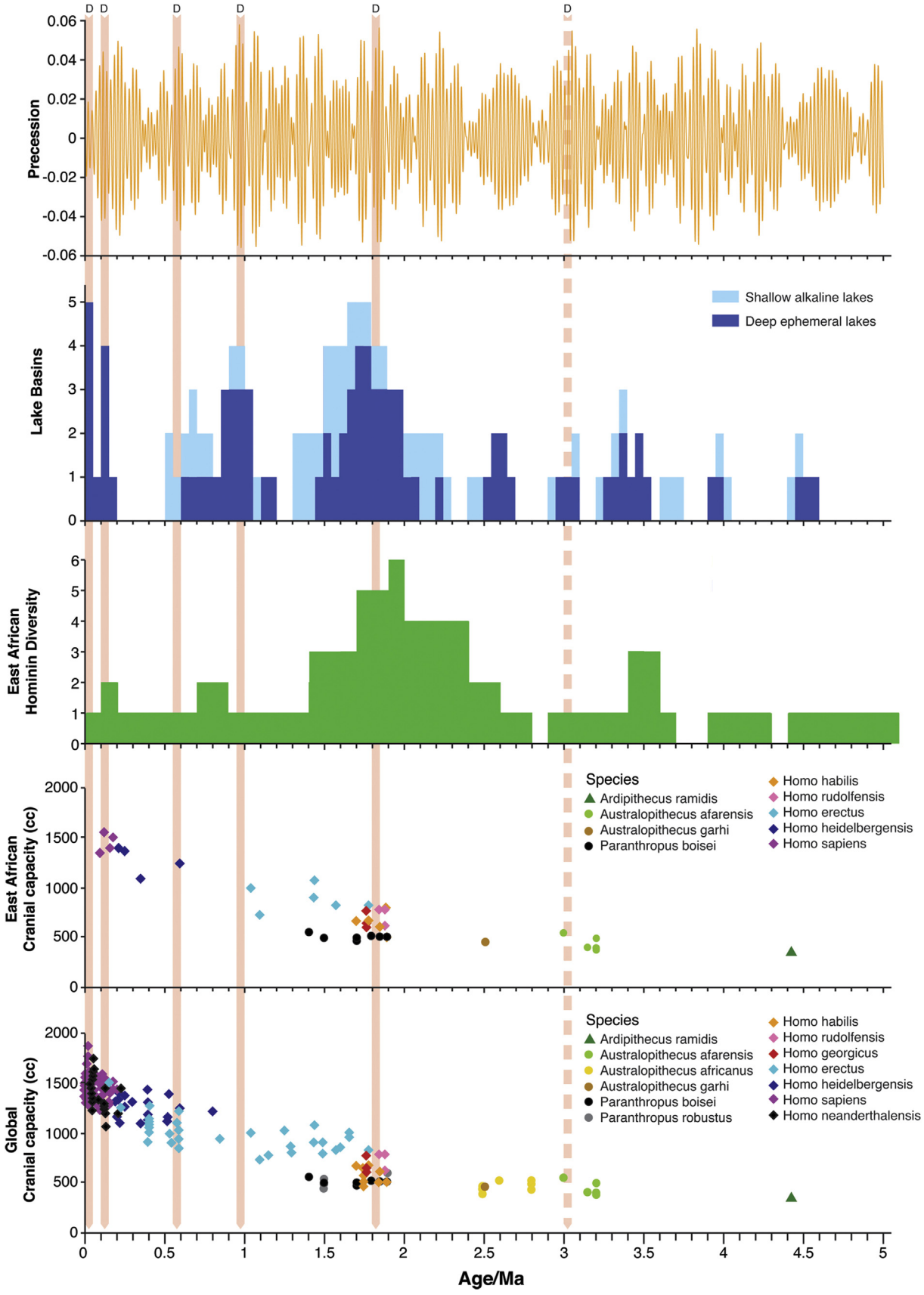

Fig. 6. Top panel shows precessional forcing followed by the East African Rift valley lake variability shown as the number of Basin containing deep or shallow lakes. Lake Basin occupation was calculated by collating the published geological evidence for the appearance of either deep ephemeral or shallow alkaline lakes in seven major Basins (see text). Middle panel shows East African hominin species diversity over time, which was calculated every 100 kyrs interval using first (FAD) and last appearance dates (FAD) from the literature (Shultz et al., 2012). Bottom panels show hominin brain capacity estimates for Africa and for Africa and Eurasia combined. Hominin specimen dates and brain size estimates were taken from Shultz et al. (2012). *Homo erectus* and *H. ergaster* were treated as a 'super-species' referred to in the Figure key and text as '*Homo erectus (sensu lato)*'. Hominin dispersal dates were estimated by FAD of hominin specimens outside of EARS and are shown by the pink bars labled 'D' (arrows show out of Africa, dotted within Africa only).

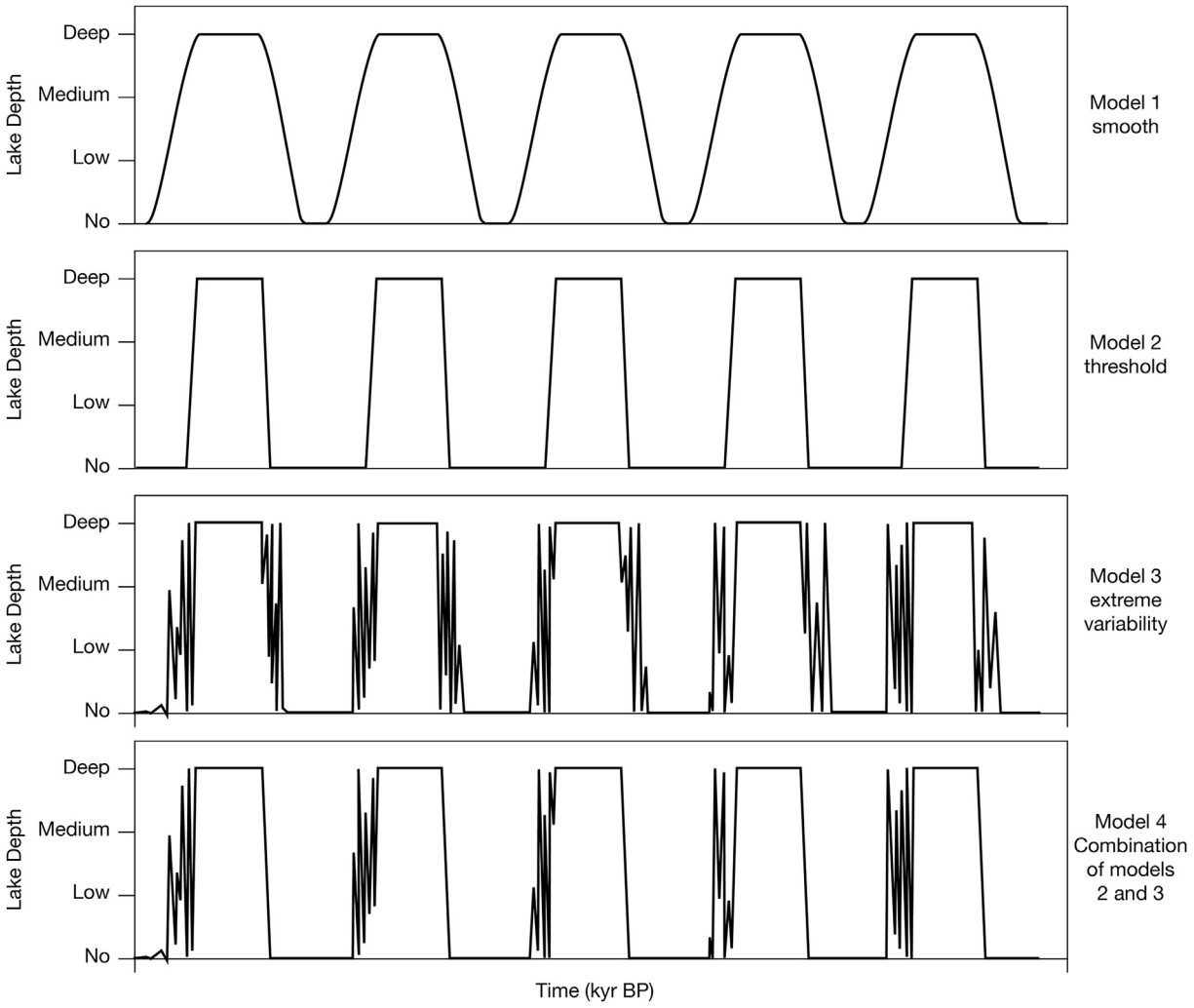

Fig. 7. Four theoretical models of possible lake changes in East Africa during the Plio-Pleistocene and their implications for the causes of human evolution (see main text). Model 1 'Smooth' and relatively slow transitions from full to no lake conditions, which would imply either high energy wet conditions or prolonged aridity may have influenced human evolution, Model 2 'Threshold' rapid transitions from full to no lake conditions which would imply the rapid transition may have influenced human evolution or the high energy wet conditions or prolonged aridity the same as Model 1, and Model 3 'Extreme variability' with highly variability during the transitions between full to no lake conditions which implies variability influenced human evolution or again the either high energy wet conditions or prolonged aridity. Combined Model has been developed base on the latest evidence from Baringo and suggests lakes appeared rapidly and then were high variable in their extent as they dried up (Wilson, 2011).

precession does not result in smooth forcing, but rather produces rapid, strong forcing periods that are combined with long periods of relatively weak forcing. If this is combined with the idea that many of the East African lakes are amplifier lakes that respond very quickly to a small increase or decrease in the precipitation-evaporation balance then it is relatively easy to envisage threshold responses of the landscape to precessional forcing (Olaka et al., 2010; Trauth et al., 2010; Borchardt and Trauth, 2011; Junginger and Trauth, 2013). In addition Potts (1998, 2013) and deMenocal (2004) also described the potential affects of millennial-scale climate fluctuations which originate in the North Atlantic but have had a profound effect on East African climate in the late Pleistocene (Brown et al., 2007; Foerster et al., 2012) and may have had an influence in the Pliocene and early Pleistocene (Wilson et al., submitted).

Fig. 7 presents four different models of theoretical lake response to local orbital forcing. The first model suggests that there is a relatively smooth and gradual transition between periods with deep lakes and periods without lakes. If this 'smooth' model is correct there may have been prolonged periods of wet or arid conditions, which may invoke the *red queen hypothesis* or the *turnover pulse hypothesis* as possible causes of evolution. The *red queen hypothesis* suggests that continued adaptation is needed in order for a species to maintain its relative fitness amongst co-evolving systems (Pearson, 2001) and that biotic interactions, rather than climate, are driving evolutionary forces. It is based on the Red Queen's race in Lewis Carroll's *Through the Looking-Glass*, when the Queen says "It takes all the running you can do, to keep in the same place" (see Barnosky, 2001). However for this to occur, a high-energy environment has to exist so that competition rather than resources is the dominant control. At Koobi Fora, there is evidence for multiple hominin species, including *Paranthopus boisei*, *H. erectus spp.*, *H. habilis* and *Homo rudolfensis* attributed to the period of maximal lake coverage (~1.8–1.9 Ma), and it may be possible that these hominins were sympatric and in competition with each other. The extreme dry periods would support the *turnover pulse hypothesis* (Vrba, 1995, 2000), with specialist species experiencing a higher extinction and speciation rate while generalists species thrived and expanded. The second model envisages a 'threshold' scenario whereby ephemeral lakes expand and contract

extremely rapidly, producing the very rapid onset of extremely dry conditions required by the *aridity hypothesis* (deMenocal, 1995, 2004). Model 2 however contains prolonged wet and dry periods and thus incorporates Model 1 as well. The third model is an elaboration of the threshold model in which there is 'extreme climate variability' during the rapid transition between deep-lake and no-lake states. Such a model would invoke extreme short-term variability that could drive speciation and extinction events, especially if this climate change occurred over a large geographic region. This would produce the widespread environmental variability as required by the *variability selection hypothesis* of human evolution (Potts, 1998). Model 3 however contains prolonged wet and dry periods and thresholds when finally lakes disappear so includes aspects of both Models 1 and 2.

Rapid stratigraphic transitions from deep lacustrine to fluvial deposition associated with the diatomite deposits from Pliocene lakes in the Baringo Basin suggest that the lakes appear rapidly, remain part of the landscape for thousands of years, then disappear in a highly variable and erratic way (Deino et al., 2006; Wilson, 2011). In fact, the absence of shallow-water (littoral) diatom species at key Plio-Pleistocene lake deposits (Kingston et al., 2007; Wilson, 2011) suggests that the lakes dried up in less than a few hundred years (see Model 4 on Fig. 7), which is consistent with the idea of a bifurcated relationship between climate and lake presence. If these preliminary results are confirmed at other sites in East Africa then the appearance and disappearance of deep-water lakes seems to follow both Model 2 and 3 (see Model 4 on Fig. 7). However, more work is required to understand how the lakes appear and disappear from the landscape if we are to link the environmental changes to specific models of evolution.

The *pulsed climate variability hypothesis* therefore takes the latest palaeoclimate understanding of East Africa and provides a framework within which to understand the causes of early human evolution. Different species or, at the very least, different emerging traits within a species could have evolved through various mechanisms including the *turnover pulse hypothesis*, *aridity hypothesis*, *variability selection hypothesis* or allopatric speciation.

8. Conclusion

Over the last two decades, intense work on African palaeoclimate and tectonics has allowed us to begin to put together a coherent picture of how the environments of eastern and southern Africa have changed over the last ten million years. The landscape of East Africa has been altered dramatically over this period of time. It changed from a relatively flat, homogenous region covered with tropical mixed forest, to a heterogeneous region, with mountains over 4 km high and vegetation ranging from desert to cloud forest. Added to this there were five major climate transitions or events, which impacted African climate: 1) the emergence and expansion of C_4 biomes (~8 Ma), 2) the Messinian Salinity Crisis (6–5.3 Ma), 3) the Intensification of Northern Hemisphere Glaciation (iNHG, 3.2–2.5 Ma), 4) development of the Walker Circulation (DWC, 2.0–1.7 Ma) and, 5) the Early-Middle Pleistocene Transition (EMPT, 1.2–0.8 Ma). The latest palaeoclimate evidence suggests that the presence of ephemeral EARS lakes is concurrent with major events in hominin evolution suggesting that we must embrace a new perspective on how environmental conditions impacted upon human evolution. Palaeoclimate information derived from stacked benthic foraminifera $\delta^{18}O$ or aeolian dust records has been unable to explain the occurrence of discrete evolutionary phases in the hominin fossil record. However, the understanding of EARS lakes as both a climate indicator and landscape feature provides this missing environmental evidence. The unusual geology and climate of the EARS introduced periods when the local environments in East Africa were highly variable. This may have driven hominin speciation and also subsequent dispersal events. The *pulsed climate variability hypothesis* should be seen as a framework, which describes the palaeoclimate context within which early human evolution occurred. It does not, however, provide a mechanism through which the evolutionary process occurred and geographic separation, environmental stress, accelerated evolution and extinction of generalist verses specialists, variability selection, and inter-species competition could all have played a role. It should also be remembered that climate may not have always been the underlying cause and that intrinsic social factors may have played a significant role especially with increased encephalisation (Flinn et al., 2005). However, it does seem that an understanding the role of East African palaeoclimates is required to explain why and when hominin species evolved and eventually migrated out of East Africa.

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