

## The East African Rift System: Tectonics, climate and biodiversity

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### Abstract

The East African Rift System (EARS) is one of the most prominent rift systems on Earth and transects the high-elevation East African Plateau. The EARS is famous for its tectonics and geology and has also been suggested to be the ‘cradle of mankind’ making it a natural laboratory for interdisciplinary research straddling the Earth and life sciences. Rifting commenced as a result of mantle plume activity under East Africa. Two distinct rift branches are observed: an older, volcanically active Eastern Branch and a younger, much less volcanic Western Branch. The Eastern Branch is generally characterized by high elevation, whereas the Western Branch comprises a number of deep rift lakes (e.g. Lake Tanganyika, Lake Malaŵi). The onset of topographic uplift in the EARS is poorly dated but has preceded graben development, which commenced at ~24 Ma in the Ethiopian Rift, at ~12 Ma in Kenya, and at ~10 Ma in the Western Branch. Pronounced uplift of the East African Plateau since ~10 Ma might be connected to climate change in East Africa and floral and faunal—including human—evolution. But linking global climate changes to biodiversity in East Africa is difficult as long-term global climate records are from marine cores off the African coast, while faunal and floral evidence from the late Miocene onwards comes from local rift valley sediments. East Africa experienced cooling starting at 15.6-12.5 Ma that heralded profound faunal changes at 8-5 Ma, when modern taxa began to take shape and the hominin lineage split from the chimpanzee lineage. The Pliocene can be divided into a period of long-term environmental stability between 5.3 and 3.3 Ma, transitioning into a period of cooler and more arid conditions after ~2.8 Ma. The end of the Pliocene warm period coincides with the earliest known stone tools at ~3.3 Ma and earliest known fossils of the hominin genus *Homo* at 2.8 Ma.

**Keywords:** continental graben, structural architecture, volcanism, topography, fossils, hominins, climate change

### 1. The East African Rift System

The East African Rift System (EARS) is more than 3000 km long and transects the high-elevation Ethiopian and Kenyan plateaus (Figure 1). This spectacular structure is a biodiversity hotspot and according to Leakey (1973) the ‘cradle of mankind’. The latter proposition highlights a conceivable link between tectonics, climate, biodiversity and hominin evolution.

The EARS is a diffuse rift system separating the Somalian Plate in the east from the Nubian Plate in the west (Calais et al. 2003). It is subdivided into an Eastern and a Western Branch (Figure 1). The Eastern Branch extends from Afar in northern Ethiopia to the Manyara Basin in northern Tanzania. Most of the Eastern Branch dissects the high-elevation Ethiopian and Kenyan plateaus (herein collectively referred to as the East African Plateau), which are separated by the Turkana depression. Lake Turkana formed in this depression and thus has an unusual tectonic position in the high-elevation Eastern Branch. It is the only large elongated rift lake in the Eastern Branch (6,405 km<sup>2</sup> surface area at an elevation of 360 m; Figure 2). In contrast, the rift lakes in Ethiopia (e.g. Lake Zway in the Awash valley, 485 km<sup>2</sup> surface area) and central Kenya (e.g. Lake Naivasha, 139 km<sup>2</sup> surface area) are situated at 1,636 m and 1,884 m altitude, respectively, and are relatively small. The Eastern Branch is magmatically very active with large shield volcanoes like Kilimanjaro, Mt. Kenya and Mt. Elgon on the rift shoulders.

The Western Branch extends from Lake Albert in Uganda to the Urema Graben in Mozambique (Figure 1) and is magmatically much less active. Basin floors have lower elevations and a number of long and deep rift lakes, indicating greater absolute basin subsidence. The largest lakes are Lake Albert (5,300 km<sup>2</sup> surface area), Lake Tanganyika (32,000 km<sup>2</sup> surface area) and Lake Malaŵi (29,600 km<sup>2</sup> surface area), all with surface elevations of ~500-800 m (Figure 2). The lake floor of Lake Tanganyika is ~700 m below sea level, and together with Lake Baikal and the Dead Sea represent the deepest continental points.

Collectively, the rift lakes of the EARS are the largest and most species-rich freshwater feature in the world (Salzburger et al. 2014). These lakes vary in age though, many of the small lakes (100-200 km<sup>2</sup> surface area) of the Eastern Branch formed since the middle Pleistocene, while Lake Tanganyika in the Western Branch formed beginning in the middle/late Miocene (Cohen et al. 1993). Lake Victoria, located in between the two rift branches, is much younger and resulted from river reversal and ponding due to pronounced rift shoulder uplift at ~0.4 Ma (Ebinger 1989). It can be described as a lake induced by rift tectonics, although it is not a rift lake.

The major differences in geography, elevation and hydrography of the EARS lakes outlined above are largely related to the tectonic development. An exception is Lake Turkana, which formed in an unusual tectonic position at the crossroads between the Eastern Branch of the EARS and the Cretaceous northwest-southeast oriented Sudan-Anza Rift system, and has geological characteristics of a ‘typical’ Western Branch rift lake in the more arid, generally high-altitude Eastern Branch.

An important question is what role these hydrographical and topographical differences play in local rift mesoclimate, biodiversity and hominin evolution. Davies et al. (1985) demonstrated that the present-day topography of the Kenyan Plateau has

a strong modifying effect on regional precipitation patterns. As a result, the Eastern Branch is relatively dry and its large savannahs today host extraordinary wildlife. In contrast, the Western Branch has mountain forests and a rich lake biodiversity. Both the lake systems and the 'sky islands' (i.e. isolated mountaintops) have produced an unusual degree of endemism among the incredible overall biodiversity. Examples include the Rwenzori Mountains (Eggermont et al. 2009) or rift lakes such as Lake Tanganyika and Lake Malaŵi (Salzburger et al. 2014).

## **2. Continental rift zones**

Continental rift zones are sites of lithospheric extension (Figure 3) (Molnar, Chapter 15). Extension is achieved through normal faulting that thins the crust. Where the brittle crust breaks continental graben (tectonically controlled depressions) develop. Dense lithospheric mantle rocks rise upward to replace the thinning crust, enhancing subsidence in the fault-bounded basins. The lithospheric mantle also extends and thins and is replaced by hotter and thus less dense asthenosphere, thereby transferring heat to the lithosphere beneath the extending region, reducing rock density and subsequently causing regional, time-dependent uplift over tens of millions of years. Mantle upwelling may be enhanced by plumes and/or small-scale mantle convection induced by steep thickness gradients at the transition between thinned and non-thinned lithosphere (Ebinger et al. 2013).

Continental rift zones are typically made up of a series of asymmetric graben. From their very inception, rift zones show regular along-axis structural segmentation into graben bounded on one or both sides by large offset border faults (Ebinger 2012). The border faults are flanked by broad uplifts that may rise 2-4 km above the surrounding regional elevations (Figure 1). Border fault length, rift flank uplift and basin dimension increase with increasing strength of the lithosphere (Weissel & Karner 1989). This is why young rift segments in strong lithosphere are characterized by long, skinny graben with deep rift lakes bounded by impressive tall escarpments.

## **3. Tectonic development of the East African Rift System**

### **3.1. African Superswell**

Africa sits above a major mantle upwelling, the African Superswell, and is breaking apart along the EARS. The African plume is rising from the core-mantle boundary (~2900 km deep) and flowing to the northeast beneath East Africa (Bagley & Nyblade 2013). Geophysical and geochemical data demonstrate that mantle upwelling and magmatism developed above an anomalously hot asthenosphere (Hart et al. 1989). This might be the reason why Africa has the highest mean elevation of all continents and why especially the Eastern Branch with its vast volcanic rock accumulations has such elevated rift floors.

The EARS comprises several discrete and diachronous rift sectors. Field data have shown that the Eastern and Western branches skirt around the Tanzania craton, an Archean/Proterozoic continental nucleus (Ring 1994). Tomographic sections show that the deep root of the Tanzania craton plays a major role in guiding the upwelling hot mantle emanating from the top of the African Superswell in the upper few hundred kilometers of the mantle (Ebinger & Sleep 1998). The earliest basaltic

volcanism in the EARS occurred between 45-39 Ma in south-western Ethiopia and northernmost Kenya (Morley et al. 1992). The widespread distribution of the volcanics suggests heating along the asthenosphere-lithosphere boundary (~100 km deep) long (~20 My) before any regional extension and surface expression of rifting (Ebinger et al. 2013).

Rift faulting started to form at ~24 Ma in Ethiopia with major extension since ~11 Ma, at ~12 Ma in Kenya, and at ~10 Ma in the Western Branch (Ebinger 1989; Ebinger et al. 2000; Corti 2009), highlighting that the ~12-10 Ma time window was important for the tectonic development of the EARS. At ~0.4 Ma a major tectonic reorganization occurred and extension became more oblique resulting in strike-slip faulting and local uplift (Strecker & Bosworth 1991; Ring et al. 1992). Rift-flank uplift at ~0.4 Ma was responsible for the formation of Lake Victoria (Ebinger 1989).

Rifting has progressed to incipient seafloor spreading in the Afar depression (Corti 2009). Further south, the Eastern Branch is superposed on the broad Ethiopian and Kenyan plateaus. The Turkana depression between the two plateaus marks a failed Mesozoic rift system, allowing for the possibility that the plateaus are part of one large zone of uplift extending from southern Africa to the Red Sea.

### 3.2. Magmatism of rift sectors

Partial melting, which is chiefly controlled by the temperature and volatile content of the asthenosphere, as well as the degree of decompression, can be used as a proxy of maturity of a rift sector (White et al. 1987; Ebinger et al. 2013). We follow Ebinger (2012) and describe those differences from the most juvenile, primitive stage in the Western Branch and the southern tip of the Eastern Branch to the most evolved stage in the Ethiopian Rift at the northern end of the Eastern Branch. The differences in volcanism, uplift and subsidence of the two EARS branches reflect the way the mantle plume was channelled underneath East Africa. The young rift sectors have not been significantly affected by plume-related heating and the entire lithosphere (tectonic plate) is strong and has not been thinned to any significant extent. The further north one goes in the Eastern Branch the longer the rift sectors have been affected by plume-related heating, leading to more pronounced igneous activity, a viscous lower crust and more advanced rifting causing weak lithosphere.

The individual rift basins of the Western Branch are long (~100-150 km) and narrow (~50-70 km). Volcanism occurs in four isolated centres (Figure 1) and commenced at  $10 \pm 2$  Ma, largely coeval with rift faulting (Ring & Betzler 1995). Overall, the morphologic and magmatic evolution of the Western Branch suggests a relatively strong plate that has been very modestly thinned and border faults penetrate the entire lower crust, consistent with deep seismicity (Figure 4a).

The Eastern Branch shows a striking progression of magmatism (and rift evolution) from south to north. The most juvenile rift sector is the Tanzanian Divergence Zone, which is ~300-400 km wide and consists of three separate graben (Figure 4b). As in the Western Branch, individual rift basins are half graben bounded by a faulted rift escarpment on one side and a flexural warp on the other (Foster et al. 1997). Each basin is ~100 km long and ~50 km wide (Ebinger et al. 1997) and contains thin (<3 km) sequences of volcanics and sediments. Most rift basins in the

Tanzanian Divergence Zone are younger than ~1 Ma (Ring et al. 2005).

The Kenya Rift further north is distinctly older and more mature than the Tanzanian Divergence Zone and forms a narrow (~50 km wide) rift sector. The basins are still asymmetric half graben and extension is of the order of 10 km with the lithosphere thinning up to ~90 km (Mechie et al. 1997) (Figure 4c). Volcanism commenced at ~23 Ma in broad downwarps that subsequently became the sites of half graben. Between 14 and 11 Ma a period of intense volcanism filled and overflowed the rift basins. Another period of pronounced volcanism occurred between 5 and 2 Ma, again overspilling the rift basins (Morley et al. 1992). A stunning feature of young volcanism is the large off-rift shield volcanoes such as Mt Elgon, Mt Kenya and Kilimanjaro in the central Kenya Rift (Figure 1). All data indicate a higher degree of lithospheric extension in the central Kenya Rift when compared to the Western Branch and the Tanzanian Divergence Zone.

The review of the various rift segments shows that with increasing maturity of the rift sectors the lithosphere thins and the amount of decompressional melt increases (Figure 4) creating weaker lithosphere. In the EARS these features are best expressed in the Main Ethiopian Rift, which links into the Afar Depression with the spreading centres of the Red Sea and Gulf of Aden.

Mohr (1983) estimated that the vast Ethiopian Plateau amounts to ~300,000 km<sup>3</sup> of volcanic rocks that erupted between 32 and 21 Ma with a short-lived period of extensive and aerially widespread flood basalts at 31-30 Ma (Corti 2009). Initial basin formation and minor extension occurred from 24-11 Ma, followed by extension in the Main Ethiopian Rift at ~11 Ma, possibly related to the onset of seafloor spreading in the Gulf of Aden and the initiation of extension in Kenya (Corti 2009). The region of active extension narrowed with time to a ~20 km wide zone near the centre of the rift since ~2 Ma. This period of rifting is probably related to seafloor spreading in the Red Sea and a re-arrangement in global plate motions at 5-3 Ma (Calais et al. 2003).

Collectively, these findings indicate that the crust beneath the rifted regions in Ethiopia has been extensively modified by magmatic processes through the addition of mafic rocks in the mid to lower crust (Figure 4d). The drastic thinning of the lithospheric mantle is probably a combined effect of lithospheric extension and plume-related thermal erosion of the lithospheric mantle. Beneath Afar, the mantle structure is much akin to that of mid-ocean ridge systems and magmatism and faulting are focused on the central rift axis (Corti 2009).

The EARS is not only an archetypal rift system; it is also a typical example of an active rift. In active rifts, rising mantle plumes cause regional updoming and thermal erosion of the lithospheric mantle and these processes are the major drivers initiating plate divergence. Plume-related processes also drive topography primarily through heat-controlled density changes and a fascinating corollary of this is that the plume-driven topography may have been an important cause of climate change in East Africa, thereby influencing the development and evolution of mankind.

#### **4. Global climate change and East Africa**

##### **4.1 Global climate in the Neogene**

The Neogene was a period of long-term global cooling and increased climate variability. Miller et al. (2011) proposed a major cooling step at ~15.5-12.5 Ma heralding the first glaciations in the northern hemisphere at 10-6 Ma (Jansen et al. 1990) and another one at 2.95-2.52 Ma causing major northern hemisphere glaciation. Global cooling and an associated aridification trend in continental Africa occurred at 3.5-3.35 Ma, 2.5-2 Ma and 1.8-1.6 Ma (Wynn 2004). Between these steps was the Pliocene warm (wet) period between 5.3 and 3.3 Ma (Tiedemann et al. 1994), with a weak east-west zonal Walker sea circulation (i.e. easterly trade winds which move water and air warmed by the sun towards the west). During the Pliocene, global surface temperature was ~3°C warmer than at present and atmospheric CO<sub>2</sub> concentrations were ~30% higher (Ravelo et al. 2004). Tropical and subtropical climates during this time significantly influenced the evolution of Pliocene biodiversity in East Africa.

The most significant global climate event of the Pliocene was the onset of significant Northern Hemisphere glaciation and a shift in the dominant period of climate oscillation, both of which commenced by ~2.8 Ma (Martinez-Boti et al. 2015; Abels & Ziegler, Chapter 20). Wet phases became less frequent after 2.8 Ma. Changes reflect a shift from orbital precession (23 ka) to obliquity (41 ka). The development of strong Walker circulation took place in two steps, neither of which is temporally linked with the onset of Northern Hemisphere glaciation. The first step, at 4.5-4 Ma, was marked by altered surface water gradients and ocean circulation, possibly connected to restriction of the Panamanian and Indonesian seaways (Cane & Molnar 2001; Molnar 2008; Pfister et al. 2014). The second step, at 2-1.5 Ma, established strong Walker circulation, a steeper sea surface east-west temperature gradient across the Pacific and initiated the modern tropical climate system (Ravelo et al. 2004). Overall, while the onset of significant Northern Hemisphere glaciation occurred as subtropical conditions began to cool, changes in the Pliocene tropical climate system were independent to some degree (Ravelo et al. 2004).

#### 4.2. Possible drivers of climate change in East Africa prior to hominin evolution

Sepulchre et al. (2006) speculated that 'massive eastern African topographic uplift' led to a pronounced reorganization of atmospheric circulation and caused increased aridification in East Africa. However, the development of pronounced topography of the rift shoulders, used as evidence in their study, has not been dated and palaeoelevation is largely unconstrained. Current work strongly suggests that pronounced rift-shoulder uplift occurred much too recently to explain late Mio/Pliocene climate shifts (Foster & Gleadow 1993; Ring 2008; Bauer et al. 2010, 2013, 2016).

A more significant factor that may have influenced East African climate in the late Miocene appears to be the topography exerted by the development of the African Superswell. Moucha and Forte (2011) developed a numerical simulation based on flow pattern changes in the mantle that allows for the reconstruction of the amplitude and timing of topographic uplift above the African Superswell through time. Their results suggest that geographically extensive (~5 x 10<sup>6</sup> km<sup>2</sup>) topographic uplift in excess of 500 m of elevation started to develop by 15 Ma and became pronounced at

10 Ma. Wichura et al. (2010) documented extensive topography in the Kenya Rift by 13.5 Ma and Gani et al. (2007) between 10-6 Ma on the Ethiopian Plateau. Major surface uplift of the East African plateau is probably causally connected with extensive volcanism in the Kenya Rift by 14-11 Ma and the surge of rift faulting in Kenya and Ethiopia at 12-11 Ma.

These findings provide evidence that topography in East Africa coincided with climate changes in East Africa and may have influenced a shift towards colder and more arid conditions by 15-10 Ma. However, further evidence for the timing of topography is needed to better evaluate tectonic drivers of climate change in Africa in the Miocene. Furthermore, a deeper understanding of the causes for climate shifts in Africa also needs to consider more global drivers, such as the Asian monsoon.

The combination of isotopic shifts, expansion of grassland at the expense of forests and suggestions of increased aridification concur with a shift near 10 Ma in South Asian climate toward today's monsoonal climate (Kroon et al. 1991; Molnar et al. 2010) largely concurrently with the increased abundance of C<sub>4</sub> plants (tropical grasses, sedges) in East Africa (Cerling 2014). If monsoon winds did strengthen, sea-surface temperatures would have dropped if the thermocline was deeper at ~10 Ma than it is today, as Philander and Fedorov (2003) suggested. Colder sea-surface temperature in the Indian Ocean off the East Africa coast would have deflected moisture transport away from East Africa towards southeast Asia, which collectively may have cooled East Africa and caused a shift towards arid conditions. A final element in the global climate mix might be the glaciers that started to grow in the Northern Hemisphere by 10-6 Ma.

#### 4.3 More recent drivers of East African climate change

The next profound change in climate took place in the mid/late Pliocene. Geo- and biochemical datasets as well as climate models have shown that East African aridification is primarily controlled by Indian Ocean sea surface temperature (Cane & Molnar 2001) and that precessional variations in C<sub>3</sub> (mostly trees) and C<sub>4</sub> plants have been controlled by changes in monsoonal precipitation driven by changes in low-latitude insolation (Philander & Fedorov 2003). These findings imply that East African climate change since ~2.8 Ma has largely been governed by ocean-atmosphere interactions in the low latitudes. Consequently, Cane and Molnar (2001) argued that changes in surface-ocean circulation, controlled by the final closing of the Indonesian seaway at ~4-3 Ma, were responsible for aridification of East Africa. According to their model, the northward motion of Australia and the associated northward displacement of New Guinea switched the source of flow through Indonesia from warm South Pacific to relatively cold North Pacific waters. This in turn decreased sea surface temperatures in the Indian Ocean leading to reduced rainfall over East Africa (Cane & Molnar 2001). The Cane and Molnar hypothesis can be seen as a novel alternative to the commonly held opinion that the onset of significant Northern Hemisphere glaciation was the main driver for aridification in East Africa (deMenocal 2004).

The second-order climate changes in the Pleistocene, namely the wet phases at 1.9-1.7 Ma and 1.1-0.9 Ma, coincide with the intensification of the Walker circulation

(1.9-1.7 Ma) and the mid-Pleistocene revolution (1.0-0.7 Ma) (Trauth et al. 2007). High-latitude forcing is required to compress the Intertropical Convergence Zone so that East Africa becomes locally sensitive to precessional forcing, resulting in rapid shifts from wet to dry conditions (Maslin et al. 2015).

Together, the evidence suggests that there was no unique cause-and-effect scenario for the evolution of hominins. Instead, it may have been a combination of many geological events—such as the changing East African topography, the closing of the Indonesian throughflow, the Asian monsoon, and Northern Hemisphere glaciation—and the importance of local rift valley climate regimes under which the key innovations leading to hominin evolution occurred.

## **5. Biodiversity in the East African Rift lakes**

The record of lake and flood plain environments in the rift basins provides important information on both the former aquatic and terrestrial habitats in the EARS. Fossils further add to our knowledge of past environments in the region. In addition, the sedimentary record of the rift lakes reflects the interplay between tectonics and climate. Tectonics also controls sedimentary patterns and explains why some lake sediments are exposed and others are not. The latter is especially important when it comes to interpreting fossil biodiversity, which is usually hampered by taphonomic biases (Behrensmeyer et al. 2007). Here we look at the response of fauna (including hominins) and flora in the EARS throughout the Neogene.

### **5.1. Lacustrine fauna**

The five largest EARS lakes (total surface area of  $\sim 146,000 \text{ km}^2$ ) contain a combined  $\sim 1,800$  species, of which  $\sim 95\%$  are endemic to a single lake (Salzburger et al. 2014). In contrast, the five North American Great Lakes (combined surface area of  $\sim 244,000 \text{ km}^2$ ) have 176 species, of which only 3% are endemic to a single lake. This disparity is largely a result of the tectonic history of the region. Furthermore, in the EARS there is a striking correlation between biodiversity and lake size (Figure 5), again highlighting stark differences between Eastern vs. Western branch lakes. Ancient lakes, like Lake Tanganyika, are hot spots of diversity and endemism.

In the EARS lakes very few species occur in more than one of the lakes. For instance, not a single cichlid species is naturally shared between lakes Malaŵi and Tanganyika. The rift lakes with their high levels of endemism and their restricted geographical occurrence are quasi eco-insular systems (Salzburger et al. 2014). They are to aquatic organisms what oceanic islands are to terrestrial biota. Ocean islands (as the EARS) are mantle plume related and terrestrial biodiversity shows an age progression in relation to plate motion over the plume, as shown by many studies from the Galapagos, Hawaii and other plume-related ocean islands (Merten 2014; Harpp et al. 2014).

The lakes are quasi-replicate systems in which closely related faunas evolved through iterative evolution. In lakes Tanganyika and Malaŵi, a whole set of similar cichlid ecotypes have evolved independently and in parallel (Kocher et al. 1993). Biodiversity in the EARS lakes is primarily controlled by the age of the lake,

topography, subsidence history, climate and river in- and outflow (Van Bocxlaer et al. 2008). The taxonomic diversity, endemism and morphological disparity are primarily the product of evolutionary radiations (reviewed in Salzburger et al. 2014). A major factor for the extraordinary levels of genetic diversity and morphological disparity is the long-term stability of the large EARS lakes (Figure 5).

Salzburger et al. (2014) showed the transience of freshwater connections and drainage patterns as a function of rift tectonics (Figure 6). Biodiversity in more stable lakes (e.g. Tanganyika and Malaŵi) contrasts with lakes of more limited ecological stability (Eastern Branch lakes or Lake Kivu) (Hauffe et al. 2014). The faunas of stable lakes are often characterized by species flocks endemic to the lake, whereas less stable lakes contain relatively more taxa that are inherited from large-scale biogeographical connections (Schultheiß et al. 2009).

A combination of tectonic and topographic changes with climatically driven cycles of aridity and humidity has periodically changed dispersal rates of both terrestrial and aquatic organisms (Danley et al. 2012). For example, during the Quaternary, Lake Rukwa had multiple highstands and spilled over into Lake Tanganyika causing exchange of faunal taxa that were previously endemic to a single lake (Cohen et al. 2013).

In the Western Branch, an extensive rift lake, Lake Obweruka, formed by 8 Ma (Pickford et al. 1993) and occupied an area from the northern end of present Lake Albert to the southern end of Lake Edward (Figure 6). Lake Obweruka persisted for ~5.5 Ma and was the site of remarkable evolutionary activity, especially among molluscs and their chief predators, fishes.

The regional surroundings of Lake Obweruka consisted of humid biotopes, including tropical forest and typical forest-savannah mosaics (Pickford et al. 1993). Strong enrichment of iron in thick lateritic soils, vertical and lateral transport of dissolved iron by groundwater, and its precipitation at the groundwater-lakewater chemocline indicates a wet tropical climate when Lake Obweruka formed (Roller et al. 2010) suggesting that the lake was meromictic (i.e., had layers of water that do not intermix) from 8 Ma (Van Damme & Pickford 1995). Overall, there was a change from a semi-arid climate before ~8 Ma to a wet climate with times of high seasonality thereafter. This highlights the importance of local rift climate as, in general, there was a shift towards increased aridity in East Africa after 8 Ma. At ~2.5 Ma, the uplift of the Rwenzori Mountains commenced and progressively split Lake Obweruka into lakes Albert and Edward (Pickford et al. 1993). Some molluscs and fish initially survived the reorganization of the lakes but eventually their diversity collapsed (Van Damme & Pickford 1995). Brachert et al. (2010) demonstrated through  $\delta^{18}\text{O}$  signatures of hippopotami teeth that the commencing uplift of the Rwenzori Mountains at ~2.5 Ma did not result in a growing rain shadow. The missing rain shadow is interpreted to be due to the overriding effect of evaporation on  $\delta^{18}\text{O}$  responding to aridification of the basin floor by a valley air circulation system through relative deepening of the valley. This again shows that mesoscale climate in rift valleys is an important factor.

The development of the Lake Victoria cichlid superflock after the Last Glacial Maximum at ~12.5 ka shows hydrological connections between Lake Victoria and

lakes Albert, Edward and Kivu in the Western Branch (Elmer et al. 2009). Presently, there is much more limited hydrological connectivity between the Western Branch lakes and Lake Victoria via the Nile River (Schultheiß et al. 2014).

## 5.2. Terrestrial fauna and flora successions in relation to lake development

We present the terrestrial fauna, mainly mammals, and flora together because they are intimately related as a number of animals feed on the vegetation. A fundamental aspect of the floral evolution in the wider EARS, especially in conjunction with hominin evolution, is the relationship between C<sub>3</sub> and C<sub>4</sub> plants (Cerling et al. 2013).

### 5.2.1 Mid Miocene

During this period a gradual replacement of subtropical forested environments by more seasonal, open country savannah-mosaic habitats took place (Bonnefille 2010). One of the best-exposed mid Miocene strata in the EARS is at Tugen Hills in the Baringo Basin of the Kenya Rift (Figure 1). The sediments yielded primate fossils at ~15.5 Ma and ~12.5 Ma that retained their primitive characters typical of their 15 Ma predecessors (Hill et al. 1991, 2002). In the younger part of the sedimentary sequence crocodiles, Hyaenidae, Felidae, pigs, rodents, bovids, giraffe, Proboscidae (elephants) and Rhinocerotidae also occur.  $\delta^{13}\text{C}$  values of tooth enamel of Rhinocerotidae and Proboscidae suggest a minor dietary component of C<sub>4</sub> grasses at ~15 Ma (Morgan et al. 1994). Environments in the Baringo Basin were mostly tropical moist or wet forest in the tropical lower montane or premontane forest category during the 15.5-12.5 Ma period (Jacobs & Kabuye 1987). Rodent assemblages from the early to middle Miocene indicate faunal stability during this period in the Baringo Basin (Winkler 2002).

### 5.2.2 Late Miocene

The next critical interval in biodiversity evolution is the 8-5 Ma period when a dramatic change in African biota took place. This period is characterized by a major faunal transition which post-dated widespread volcanism in Kenya at 14-11 Ma, major rift faulting in Kenya and Ethiopia at ~12-11 Ma and the formation of the Western Branch at ~10 Ma. The latter had a profound impact on East African lacustrine evolution as at least two major long-lived lakes (Tanganyika and Obweruka) formed in the late Miocene.

Shrinkage of the equatorial forests coincided with an expansion of C<sub>4</sub> plants (Cerling et al. 1997). In Africa, this resulted in the emergence of the mammal elements that would dominate the late Cenozoic including hippos, giant pigs, grazing antelopes, true giraffes and elephants, and hominins. Faunal assemblages during the 8-5 Ma period are transitional, reflecting the replacement of mid Miocene communities containing creodonts (carnivorous mammals), climacoceras (large mammals), caprins (goat-like animals) and boselaphines (antelopes) with more modern tribes (Kingston et al. 2002). By ~5 Ma faunas were distinctly different to mid Miocene ones in East Africa and also Asia (Hill 1999). These profound changes are linked to two main factors: (1) migratory exchange with Eurasia and (2) gradual

replacement of subtropical environments by more seasonal open country savannah-mosaic habitats considered characteristic of the latest Miocene (Leakey et al. 1996; Cerling 2014).

In Tugen Hills, sediments dated between ~7.5 and 6.2 Ma show the earliest change towards the modern fauna. New families such as elephantids, modern rhinoceros, hippopotamids, giraffids, bovids and the first leporids in sub-Saharan Africa appear (Kingston et al. 2002). Associated with the faunas are fossil wood fragments representing six taxa (Kingston et al. 2002). Living representatives of the fossil taxa show fairly limited environmental tolerance and suggest that the fossil forest grew in a lowland or upland forest with floral affinities to West and Central Africa. Maximum tree heights were >50 m, a height typical for wet or moist forest communities (Menaut et al. 1995), as drier African forests and montane forests have tree heights <35-40 m (Richards 1996). At Lothagam, palaeosols document a period of increased aridity between ~6.7 and 5 Ma and depositional stasis at ~6.5-5.2 Ma is indicated by two very well developed luvisols (Wynn 2004). Vegetation throughout the interval appears to have been a mosaic of floodplain savannahs dissected by gallery woodland.

Nonetheless, fossil remains are rare in the 8-5 Ma interval of the EARS, and the tempo and mode of change during this important transitional period is therefore poorly known (Kingston et al. 2002). However, molecular data can help to fill this gap, and phylogenies of snakes (Menegon et al. 2014) and fishes (Dorn et al. 2014) suggest that tectonic processes might have triggered speciation events in these groups at this time.

### 5.2.3 Pliocene

The Pliocene warm (wet) period had a pronounced impact on lacustrine conditions and more large lakes formed by 4.5-4 Ma (Malaŵi and Lonyumun). However, there is no known tectonic driver for climate change during this period. Nonetheless, the formation of lakes Lonyumun and Malaŵi and the important lake stage of Obweruka at 4.5-4 Ma coincided with the first step in the development of strong Walker circulation. If this first step in Walker circulation was indeed related to processes restricting and finally closing the Indonesian and Panamanian seaways (see above) (Jaramillo, Chapter 22), then global tectonic processes can be linked to major shifts in hydrography in East Africa in the early Pliocene.

The faunal and climatic proxies for the Pliocene warm period show wet conditions coinciding with extensive highstands of rift lakes and the existence of palaeolakes Obweruka in the Albertine Basin, and Lonyumun in the Turkana Basin (Figure 6). During this time, the fauna of the northern Malaŵi Rift of the Western Branch was dominated by typical modern African equids, suids, hippopotamids, giraffids, bovids, elephantids and rhinocerotids (Sandrock et al. 2007). The high percentage of terrestrial species (~90%) suggests a tropical semi-arid bushland or tropical grassland environment. Towards the end of the Pliocene the faunas indicate a strong trend towards arid grassland that persisted into the Pleistocene (Sandrock et al. 2007).

Lüdecke et al. (2016) presented a long-term Plio-Pleistocene  $\delta^{13}\text{C}$  record from

pedogenic carbonate and suidae (pig) teeth of the northern Malaŵi Rift. The sediments contain fossils of *Homo rudolfensis* (Schrenk et al. 1993) and *Paranthropus boisei* (Kullmer et al. 1999). Consistent  $\delta^{13}\text{C}$  values of -9‰ indicate a  $\text{C}_3$  dominated closed environment with regional patches of  $\text{C}_4$  grasslands. The overall fraction of woody cover of 60-70% reflects more forest canopy in the Malaŵi Rift than in the Eastern Branch. The appearance of  $\text{C}_4$  grasses is considered to be a possible driver of evolutionary faunal shifts (Cerling et al. 2013). However, despite the different climatic and ecosystem evolution in the north (e.g. Kenya) and in the south (Malaŵi), similar hominins and suids occurred in both landscapes (Bromage et al. 1995), pointing to habitat flexibility and/or micro-habitat tracking, which may also indicate their nutritional versatility (Lüdecke et al. 2016).

#### 5.2.4 Pleistocene

East Africa became cooler and more arid after ~2.8 Ma. Vrba (1988, 1999) proposed a major turnover pulse in EARS mammals at ~2.8 Ma linked to the origin of hominin genera *Paranthropus* and *Homo* and the extinction of *Australopithecus*. Despite the fact that some causes of faunal turnover during the late Pliocene seem reasonably well established (Reed 2008), a number of technical difficulties in recognizing faunal patterns have been proposed, e.g. related to the resolution of time scales (Faith & Behrensmeyer 2013), stratigraphic gaps and sampling errors (Frost 2007). Nevertheless, in recent studies, faunal turnover events were established to have occurred around 2.8 Ma at Afar (DiMaggio et al. 2015), and around 2.0-1.75 Ma on a larger African scale (Bibi & Kissling 2015).

Vrba (1999) also proposed a turnover pulse among bovids at 2.8-2.5 Ma. Suids do not seem to show an increased amount of turnover at this time (White 1995). This discrepancy may be the result of the difference in trophic ecology between these groups. The bovids may have been relatively specific in their habitat requirements, dividing the ecosystem into several niches, whereas the suids may have been broader in theirs. Suids are eurybiomic (tolerating variable habitats), and therefore were not affected by a possible 2.8-2.5 Ma turnover event (Frost 2007). In mammals, herbivory (i.e., plant eating) generally leads to fast speciation rates during periods of climatic fluctuations (Hernandez Fernandez & Vrba 2005), whereas omnivory (eating both plants and animals) results in reduced diversification rates. The origins of *Paranthropus* and *Homo* at around 2.5 Ma are directly linked to changes in diet availability (Bromage & Schrenk 1999).

All possible events of increased turnover at 3.5 Ma, 3 Ma, 2.8-2.5 Ma and 2.0-1.75 Ma occur at periods where there are also possible stratigraphic gaps, even in the larger data sets. Forest fragmentation may have been important in speciation and diversification. Thus, while climate change may have been a significant factor in faunal evolution, it seems that global cooling between 2.8-2.5 Ma alone did not necessarily cause a faunal and hominin turnover pulse.

## 6. The advent of hominins

### 6.1 Hominins and their ecological context

Hominin fossils are exceedingly rare in the geological record. Therefore, detailed aspects of their evolution, as reflected in patterns of distribution and diversification, are not well resolved. Moreover, climatic and environmental factors that drove the chimpanzee/hominin split and the consequent evolution of hominins remain poorly known. A challenging problem in hominin research is therefore to relate tectonics and both global and regional climate changes to shifts in palaeoenvironments and species occurrences, dispersal and evolution (Behrensmeyer 2006; Potts 2007; Levin 2015).

All but a very few hominin fossils in the EARS are from the Eastern Branch (Bonnefille 2010) with the northern part of the Malaŵi Rift (Schrenk et al. 1993) and the Albertine Rift (Crevecoeur et al. 2014) being the only localities so far where hominin remains have been discovered in the Western Branch (Figure 7). Widespread lake formation led to more diverse environments, which potentially influenced the evolution of hominins by altering their habitat. However, it is questionable whether the EARS basins were indeed the only sites where our ancestors evolved. The discovery of abundant fossils in the EARS might be taphonomically biased, as it is basically in the rift basin ‘badlands’ where sediments of the right age occur, with reasonable potential for preservation and discovery of hominin fossils (Ring 2014).

Hill (1995) suggested that the human ancestor must have been an ‘anthropomorphic ape’ that lived during the Miocene, probably before 7.0–6.5 Ma. When and where did the major evolutionary transition to hominids take place? Most likely not only in the EARS, but also in early wooded savannah ecosystems, developing all around the diminishing African rainforest towards the end of the Miocene (Schrenk et al. 2004; Bonnefille 2010). As Hill (1995) noted, only 0.1% of Africa is represented by fossil localities, providing perspective on the scale of knowledge versus the huge area of diverse habitats where early hominins evolved. However sparse this record might seem, most of the available evidence indicates that environmental changes in Africa, driven by tectonics and climate, have had a profound impact on early human evolution and probably paced these transitions in our early history.

Vertebrate faunas provide important evidence for the ecological context of hominin evolution over a wide range of scales, from site-specific analysis of taxa directly associated with hominin fossils to faunal trends indicating long-term environmental change that could have affected human evolution (Behrensmeyer et al. 2007; Macho 2013; Potts 2013). Site-specific faunal information from fossil records can address palaeoecological questions at local (Cooke 2007), regional (Bobe et al. 2007; Sandrock et al. 2007) and continental scales (Frost 2007). However, a major issue is the discontinuity between local stratigraphic records and their relation with global-scale processes (Bibi & Kiessling 2015).

An additional problem in this context is that most available long-term climate records are based on marine core data from basins proximal to Africa (Tiedemann et al. 1994; deMenocal 2004; Feakins & deMenocal 2010), while most of the late Miocene and Pliocene hominins and other fauna occur in continental deposits of the EARS and further west in the Chad Basin. In response to this issue, researchers increasingly attempt to obtain climate proxy records directly from outcropping hominin-bearing deposits (Kingston et al. 2002; Joordens et al. 2013; Cerling 2014).

For bypassing the problematic characteristics of outcrops (such as diagenesis and stratigraphic discontinuity), cores have been drilled into lakes and ancient lake sediments to allow the capture of relatively pristine and continuous climate records that can be correlated to fossil records (Cohen et al. 2016).

## 6.2 Chronology of hominin findings

The first African hominin remains were found in 1921 in Zimbabwe (Woodward 1921) and 1924 in South Africa (Dart 1925)—outside the EARS. Thousands of hominin fragments, comprising roughly 10 genera and 20 species, have been discovered at more than 50 African sites (Figure 7). The majority of specimens originate from South African cave fillings. Whereas caves have the advantage of a higher preservation potential, EARS sites are generally more accurately dated. Two of the major evolutionary breakthroughs of human evolution in Africa are the origin of bipedal locomotion between 8 and 6 Ma, and the onset of cultural evolution at ~3.3 Ma.

The oldest hominin species found so far, *Sahelanthropus tchadensis*, is from the Chad Basin about 2500 km west of the EARS (~7 Ma; Brunet et al. 2002) (Figure 7). This age broadly fits with the chimpanzee-hominin divergence estimated at 8-6 Ma (Patterson et al. 2006; Steiper & Young 2006; Langergarber et al. 2012). Other late Miocene hominins are *Orrorin tugenensis* from the Kenya Rift (6-5.7 Ma, Pickford & Senut 2001) and *Ardipithecus kadabba* (5.8-5.2 Ma, Haile-Selassie 2001) from Afar. The oldest Pliocene (4.4 Ma) hominin, *Ardipithecus ramidus*, is also from Afar (White et al. 2009).

Fossil remains, whose attribution to the hominin lineage are unambiguous, belong to the genus *Australopithecus* and are known from ~4.2 Ma onwards. They derive mainly from the Eastern Branch and South Africa (Wood & Lonergan 2008) with the exception of *Australopithecus bahrelghazali* (Brunet et al. 1995; Strait 2013) from northern Chad. The youngest Pliocene hominin fossil at 2.8-2.75 Ma is from the northern Ethiopian Rift and so far represents the earliest appearance of the genus *Homo* (Villamoare et al. 2015). The earliest record of stone tools just post-dates the end of the Pliocene warm period: Harmand et al. (2015) reported stone tools from Lake Turkana dated at 3.31-3.21 Ma, discovered in the same sediments where fossils from the hominin species *Kenyanthropus platyops* were found (Leakey et al. 2001). This is broadly coeval with animal bones from Ethiopia that bear stone-inflicted cut marks, dated at ~3.39 Ma (McPherron et al. 2010).

Many of the early Pleistocene EARS hominins attributed to the genus *Homo* (Leakey et al. 2012; Spoor et al. 2015) co-occur with hominins of the genus *Australopithecus* (e.g. *Australopithecus sediba* in South Africa) as well as *Paranthropus* (Berger et al. 2010). Most of the younger (<0.3 Ma) hominin species are found outside the EARS and outside Africa (e.g. in Georgia, Lordkipanidze et al. 2013). This is interpreted to reflect that hominins dispersed 'out of Africa' between 2 and 0.1 Ma (Mithen & Reed 2002).

## 6.3. Hominins, climate and the changing landscape

Palaeoanthropologists and geologists often argue that climate changes causing a transformation from tropical forest to savannah-type habitats (change from C<sub>4</sub> to C<sub>3</sub> environments) were the main drivers of early hominin evolution. A review of Cenozoic vegetation and climate by Bonnefille (2010) concluded that an expansion of savannah/grassland at ~10 Ma in East Africa took place after the 15.5-12.5 Ma cooling event. Another pronounced change in vegetation took place at 6.3-6.0 Ma and was marked by a decrease in tree cover across all of tropical Africa.

The earliest hominins found in the Kenyan and Ethiopian Rift, and also in Chad, inhabited mixed C<sub>3</sub>/C<sub>4</sub> environments, which probably was a grassland with patches of woodland (Cerling 1992). There is no record of closed-canopy forest at localities where early hominins were found. Current interpretations of the palaeoenvironment suggest that *Orrorin* in Kenya lived in open woodland habitats with dense woodland or forest in the vicinity, possibly along lake margins. *Sahelanthropus* likely dwelled in a mosaic of environments, ranging from gallery forest at the edge of a lake, to savannah woodland, to open grassland, although there are indications that there was a dominance of shrub/bushland and grassy woodland habitats within the Chadian lake basin. *Ardipithecus kadabba* in Ethiopia lived in riparian woodland and floodplain grassland along water margins (Su 2014). WoldeGabriel et al. (1994) suggested that after 4.4 Ma hominins started to inhabit environments with more open vegetation. By contrast, a mosaic of open and wooded habitat is reconstructed by Leakey et al. (1996) for the Miocene/Pliocene boundary in the Turkana Basin just south of the Ethiopian border. The early Pliocene *Ardipithecus ramidus* is found in closed woodland habitats with possible patches of forest (White et al. 2009; Jolly-Saad & Bonnefille 2014, but see Cerling et al. 2013, for a different view) and associated with bushland and grassland habitats in the northern Ethiopian Rift (Levin et al. 2004). Combined, these habitat interpretations of the African late Miocene and early Pliocene suggest that the beginnings of our lineage did not occur in open, semi-arid to arid habitat conditions, but rather in more closed and/or wet habitats. However, a definitive conclusion is difficult to draw at this time given the lack of detailed palaeoecological reconstruction for the palaeohabitat where *Orrorin* is found, the possibility that *Sahelanthropus* was found in more open habitats, the discordance in interpretation of the Ethiopian dataset, and the general paucity of late Miocene/Pliocene hominin-bearing sites in Africa.

During the late Pliocene at ~3.5 Ma, hominin diet, especially of *Kenyanthropus*, began to include higher amounts of C<sub>4</sub> food resources (Cerling et al. 2013). By ~2.8 Ma, dryer conditions prevailed in the African landscape (Vrba 1999; deMenocal 2004). Behavioural flexibility of early hominins was likely triggered by abiotic changes (Macho 2013). Extensive open habitats with more arid-tolerant vegetation developed. The resulting selective pressures apparently led to increased survival of megadont varieties capable of feeding on tougher fruit and open woodland-open savannah food items. This is true for early hominins as well as numerous large eastern and southern terrestrial African vertebrate lineages at ~2.5 Ma (Turner & Wood 1993) and resulted in the phyletic splitting of *Australopithecus afarensis* into *Paranthropus* and *Homo* lineages after ~2.8 Ma (Bromage & Schrenk 1999; Strait et al. 2015). It appears likely that our ancestors had an eurybiomic lifestyle.

The work by Lüdecke et al. (2016) highlights major differences in ecosystems between the Eastern Branch and the Malaŵi Rift of the Western Branch in the Plio-Pleistocene. Brachert et al. (2010) demonstrated that the large water bodies entrenched between strongly uplifted rift shoulders of the Western Branch had an impact on local rift climate by creating a valley air circulation system through relative deepening of the lake basin. Bobe et al. (2007) showed that aridity trends in the Turkana and Hadar areas show different responses at different times, evidence that local geography and tectonics played an important role in mediating environmental change. This strongly suggests that mesoscale climate in rift sectors might be more important and not necessarily directly linked to global climate. These factors may also explain local climate proxy variations and different habitat reconstruction for the Miocene/Pliocene boundary in the Ethiopian/Kenya border region.

The evolution of the genus *Homo* in the early Pleistocene can only be understood by integrating fossil, archaeological and environmental data on seasonal, decadal and evolutionary time scales. In East Africa, climatic and environmental fluctuations were intensified by tectonic activity, increased landscape fragmentation and amplifier lakes (high-precipitation, high-evaporation lakes formed between graben that respond rapidly to moderate climate shifts; Trauth et al. 2010). Several scenarios and hypotheses have been put forward to explain and test processes of selection and speciation in Plio-Pleistocene hominin evolution in the context of climate change. Among others, these include the turnover pulse hypothesis (Vrba 1999) and the pulsed climate variability hypothesis (Maslin et al. 2015). The variability selection hypothesis (Potts 2007, 2013; Potts & Faith 2015), the most comprehensive approach to early hominin evolutionary patterns to date, refers to adaptive change in response to environmental variation. Whereas short-term variability takes into account habitat variations, long-term variability selection assumes that certain adaptations have evolved as a result of large, environmentally caused inconsistencies in the selective conditions.

This review highlights that, whereas the influence of climate changes can be documented in many instances, the complex interactions of various drivers of hominin and faunal evolution in space and time are not necessarily statistically solid yet. Behrensmeyer et al. (2007) summarized taphonomic biases of habitat reconstruction, especially in the deposition context. Mid/late Miocene to Pleistocene sediments are only exposed in a few rift sectors and hardly any deposits of this age occur outside the EARS. This probably results in a strong bias in reconstructing general hominins habitats. The small sample size, spatially concentrated fossil localities (i.e. lots of fossil material from the Kenyan and Ethiopian rift sectors and hardly any material from the Western Branch), and preservation biases make correlations between climate and hominin evolution speculative.

## **7. Concluding remarks: Biodiversity, hominins, climate and tectonics**

The ~10 Ma time window is of great importance for overall East African climate, biology and tectonics. At this time, the Western Branch started to form and sea-floor spreading in the Gulf of Aden caused a surge of extensional deformation in the Ethiopian and Kenya Rift. Rift structure and architecture are probably less important

for regional East African climate change. The latter appears controlled by plume-related density changes and resulting surface uplift and the strengthening of the Indian monsoon that made East Africa drier.

Regional surface uplift also largely controlled the development of the EARS lakes and the pronounced differences in lake size, depth and biodiversity between the Eastern and Western Branch lakes (Figures 2 and 6). Rift structure is important for local climate effects. Studies by Bobe et al. (2007) and Brachert et al. (2010) show that rift mesoclimate may represent an underestimated aspect in previous palaeoclimate reconstructions from rift valley data.

Can climate change, driving and controlling hominin evolution, be linked to stages in the evolution of the EARS? As outlined, numerical models of uplift above the African Superswell can broadly be linked with pronounced changes in EARS tectonics and biodiversity evolution. Significant tectonic reorganization at ~0.4 Ma coincides with the formation of Lake Victoria. Because the Lake Victoria basin is tectonically connected to rift shoulder uplift of the two EARS branches, its formation suggests enhanced uplift by 0.4 Ma. Rift shoulder uplift at 0.4 Ma was also important for uplift and exposure of rift sediments, thus creating the potential for discovering fossils. The occurrence of fossils over the continent and within the rift is influenced by preservational biases. In the rift, hominin fossils are largely found in the more arid Eastern Branch. In contrast, lake biodiversity is much more pronounced in the Western Branch with its great subsidence and wetter climate. Lake Turkana is an exception, as it is tectonically controlled by the position of a Cretaceous rift causing a depression. The tectonic differences between the Western and Eastern Branch reflect different plate strength, largely controlled by mantle-plume activity.

**Acknowledgements:** Thanks to Carina Hoorn for inviting us to put this review together and for continued editorial help. We also appreciate helpful comments and reviews by Josephine Joordens, Henry Wichura, Thomas Lehmann and Bert Van Bocxlaer, and editorial assistance by Allison Perrigo.

### **Figure captions:**

Fig.1 (colour). The East African Rift System (EARS) superimposed on the Ethiopian and Kenyan plateaus, collectively known as the East African Plateau ([www.geomapapp.org](http://www.geomapapp.org)). The EARS comprises series of individual graben that link-up to form the Western and Eastern branches. The rift floors of the Eastern Branch, with vast volcanic rock accumulations (in red), have high elevations and only the Turkana graben of the Eastern Branch has a lower elevation. Localities mentioned in the text are indicated and dotted lines for cross-sections depicted in Figure 4 are shown.

Fig.1 (greyscale). The East African Rift System (EARS) superimposed on the Ethiopian and Kenyan plateaus, collectively known as the East African Plateau ([www.geomapapp.org](http://www.geomapapp.org)). The EARS comprises series of individual graben that link-up to form the Western and Eastern branches. The rift floors of the Eastern Branch, with vast volcanic rock accumulations (in dark grey shading), have high elevations and

only the Turkana graben of the Eastern Branch has a lower elevation. Localities mentioned in the text are indicated and dotted lines for cross-sections depicted in Figure 4 are shown.

Fig.2. Elevation vs size (surface area) for the main EARS rift lakes. Lakes in the Western Branch (indicated by squares) are relatively larger and at lower elevations than those in the Eastern Branch (indicated by filled circles). Note that the data point for Lake Turkana plots in the same general area as those of the Western Branch lakes.

Fig.3. Simplified sketch showing changes in lithospheric structure during rifting. The pre-rift lithosphere at either end of the cross section is modified by faulting and magmatism in the rift. Extension thins the lithosphere causing subsidence, and asthenospheric inflow beneath the rift replaces the denser lithospheric mantle causing long-term uplift. Note the elevated transition zone between the brittle upper crust and ductile lower crust in the rift zone, caused by a thermal perturbation, especially in the magma-rich part of the rifts where mafic melt that accumulated beneath the crust (i.e., underplated) forms dikes (vertical black lines) and intrusions (black ellipses) (after Ebinger 2012). Note that underplating refers to melting that forms "ponds" beneath the crust. (see [Molnar, Chapter 15](#), for simplified version of sketch).

Fig.4. Simplified lithospheric cross sections through the Western and Eastern Rift branches showing different styles of rifting, lithospheric thinning and magmatism; for the localities of the cross-sections see the dotted lines in Figure 1. (a) Albertine Rift of the Western Branch; the lithosphere is hardly thinned and the lower crust is not viscously deforming; the chemistry of the magmatic rocks is primitive and the volume of magmatism is very limited; pronounced rift-flank uplift created the >5000 m high Rwenzori Mountains. (b) Tanzania Divergence Zone of the Eastern Branch; note the wide area affected by rifting caused by the strong lithosphere of the Massai Block; lithospheric structure similar to (a) indicating early stages of rifting. (c) Central Kenya Rift; the lithosphere is notably attenuated and thinned, resulting in a viscous lower crust in which the high-angle upper crustal normal faults flatten out; note off-axis volcanism that forms large volcanic edifices like Mt. Kenya on the rift shoulder. (d) Main Ethiopian Rift; the most advanced stage of continental rifting, resulting in strongly thinned lithosphere; the style of rifting becomes more symmetric and rifting is strongly assisted by pronounced magmatism.

Fig.5. Lake size and ecosystem stability vs. species diversity in the EARS lakes shows a positive correlation. The metric indicates that the large Western Branch lakes, and also Lake Victoria, are stratified and biodiversity hotspots. The high biodiversity in Lake Victoria is possibly due to invasion history, intrinsic biological factors and the saucer-like (non-rift) basin morphology. Holomictic, completely mixed; meromictic, permanently stratified; the dotted line with a question mark indicates the unknown size of Lake Obweruka (after Salzburger et al. 2014).

Fig.6 colour. Palaeogeographic maps of the EARS lakes showing hydrographic configurations of the major lakes and rivers for four periods over the past 4 Ma: (a) ~4 Ma, (b) ~2 Ma, (c) ~100 ka and (d) ~18 ka (after Salzburger et al. 2014). The solid blue lines indicate major perennial rivers; dashed blue lines show intermittent rivers. The main drainage until ~18 ka (Last Glacial Maximum) was to the west into the Western Branch depocenters and ultimately into the Atlantic Ocean. The Lamu marine embayment was controlled by a Cretaceous rift, which also controls the Turkana depression. Note the dramatic changes in hydrography at 18 ka.

Fig.6 greyscale. Palaeogeographic maps of the EARS lakes showing hydrographic configurations of the major lakes and rivers for four periods over the past 4 Ma: (a) ~4 Ma, (b) ~2 Ma, (c) ~100 ka and (d) ~18 ka (after Salzburger et al. 2014). The solid lines indicate major perennial rivers; dashed lines show intermittent rivers. The main drainage until ~18 ka (Last Glacial Maximum) was to the west into the Western Branch depocenters and ultimately into the Atlantic Ocean. The Lamu marine embayment was controlled by a Cretaceous rift, which also controls the Turkana depression. Note the dramatic changes in hydrography at 18 ka.

Fig.7. The locations of African early hominin sites in relation to the distribution of EARS lakes. Hominin sites outside of the EARS are known mainly from the Lake Chad Basin (Mio-Pliocene sites at Toros Menalla, Koro Toro, Yayo), from cave deposits in South Africa (Plio-Pleistocene) and from north-western African sites (Pleistocene). Light grey dots on the continent indicate topography, grey lines show major rivers and lakes.

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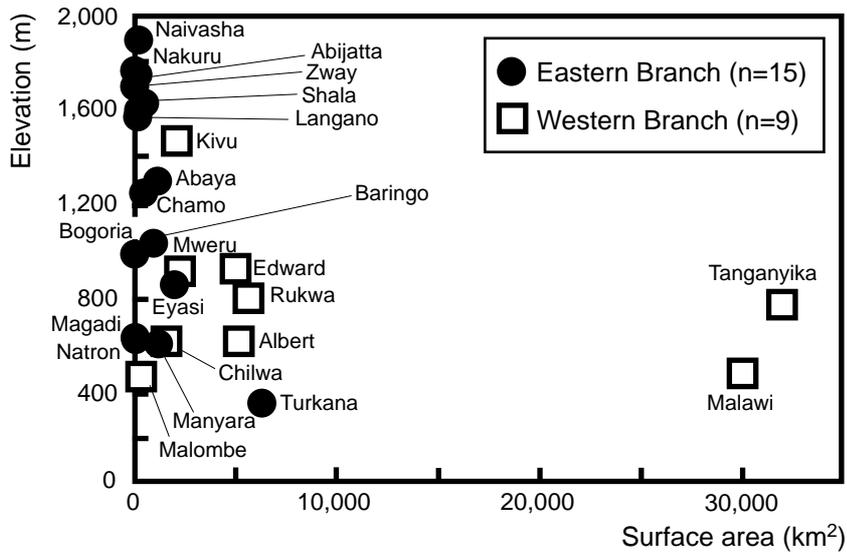
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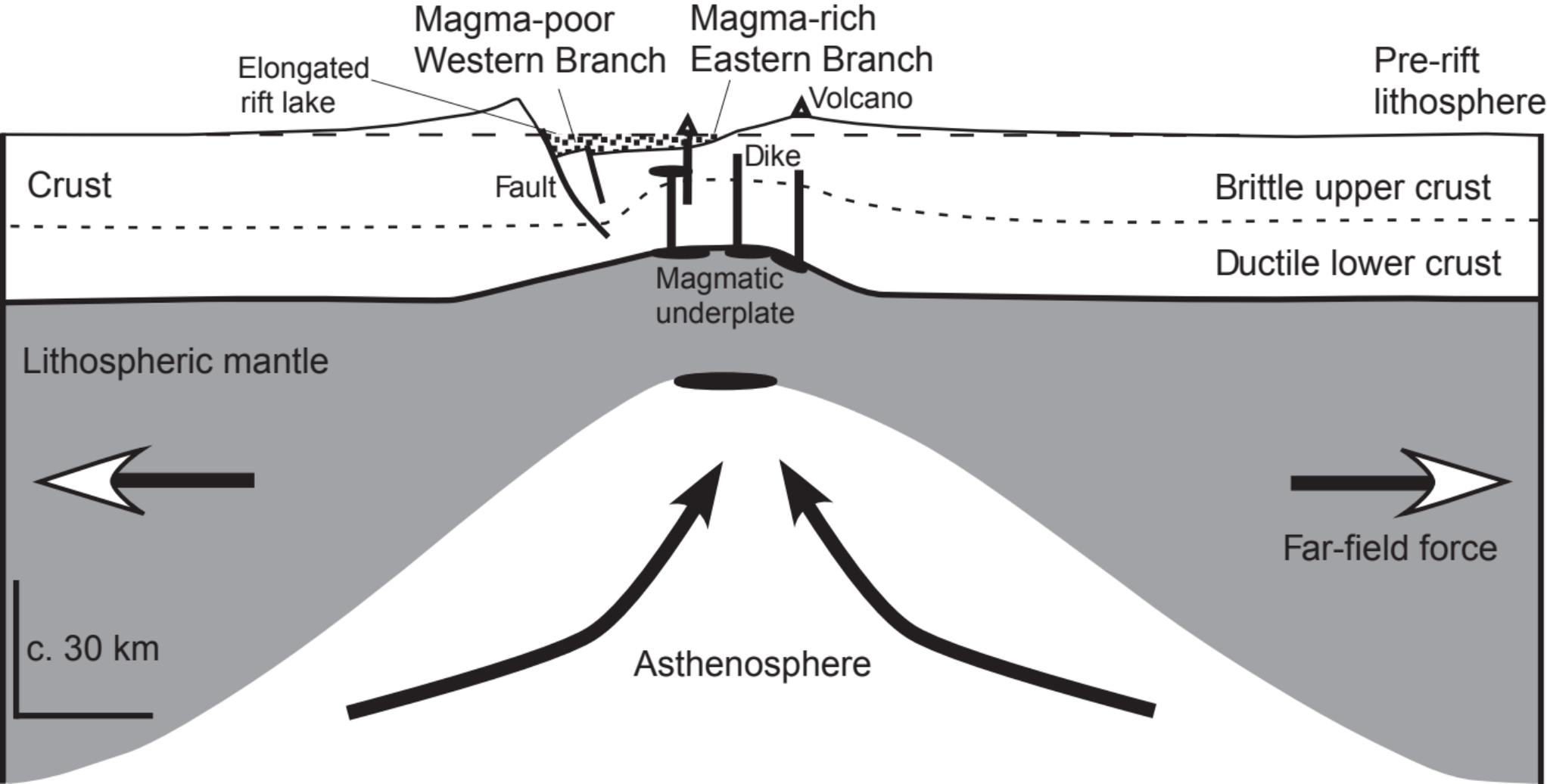
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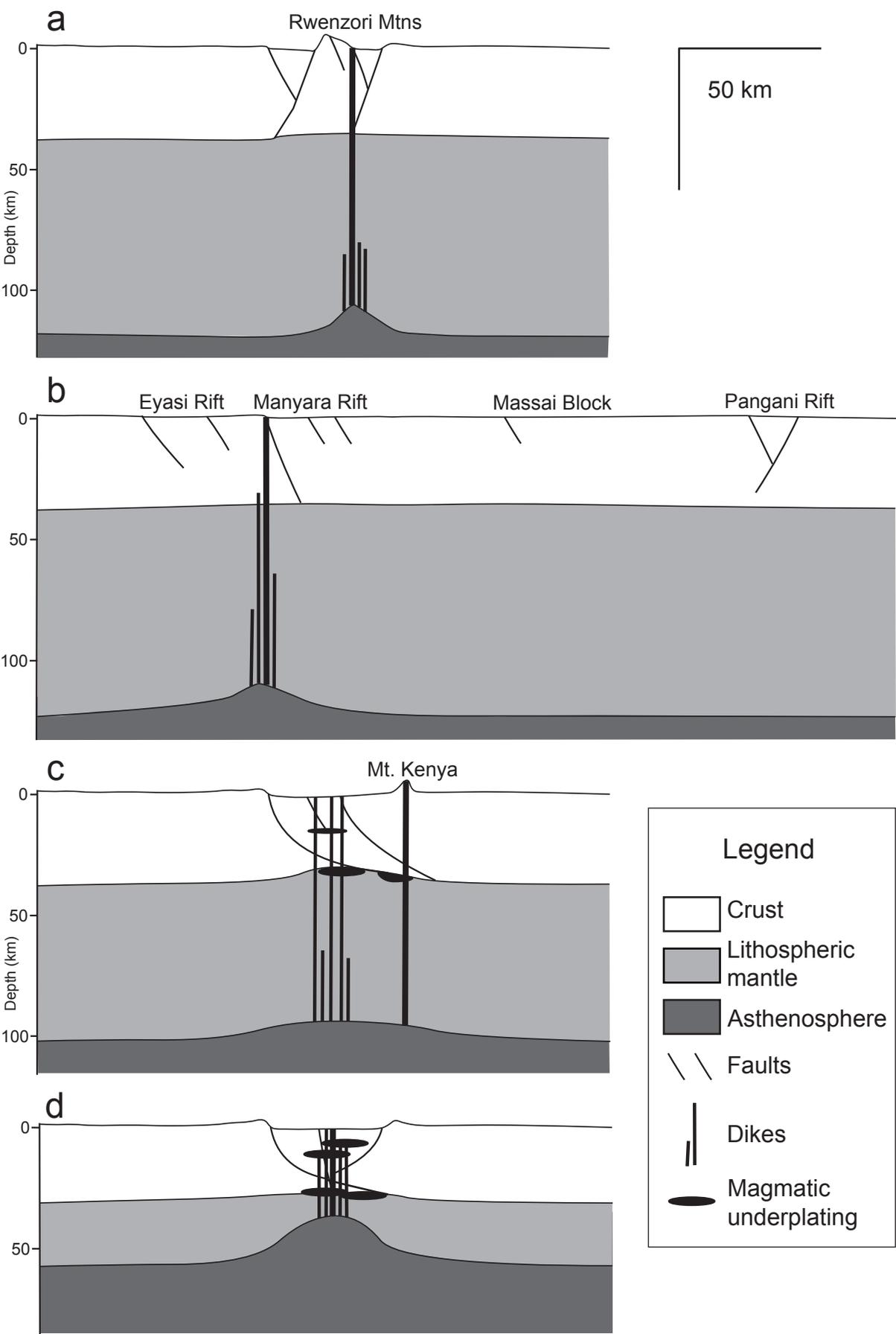
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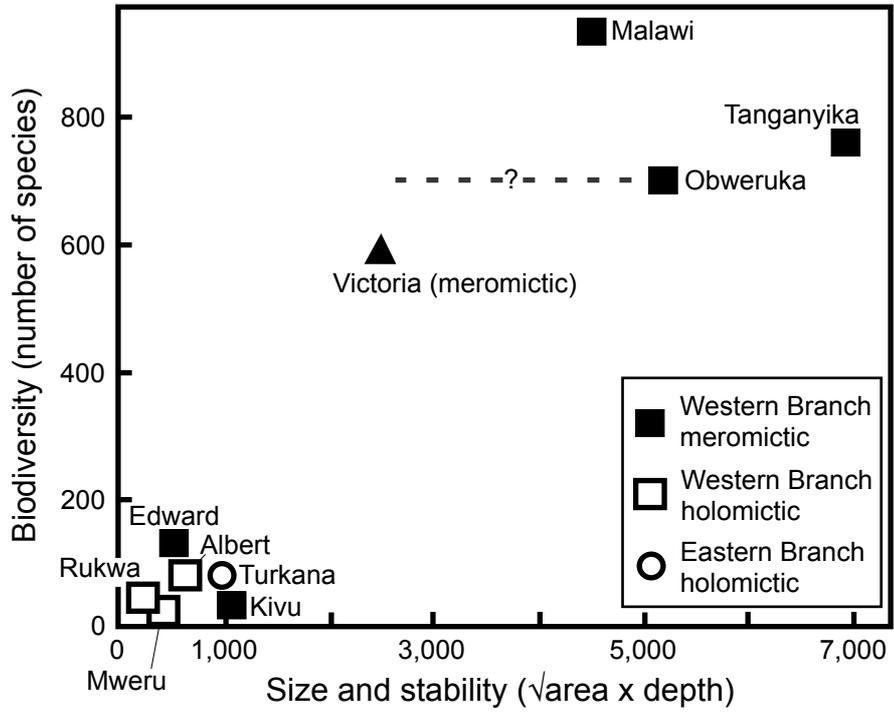
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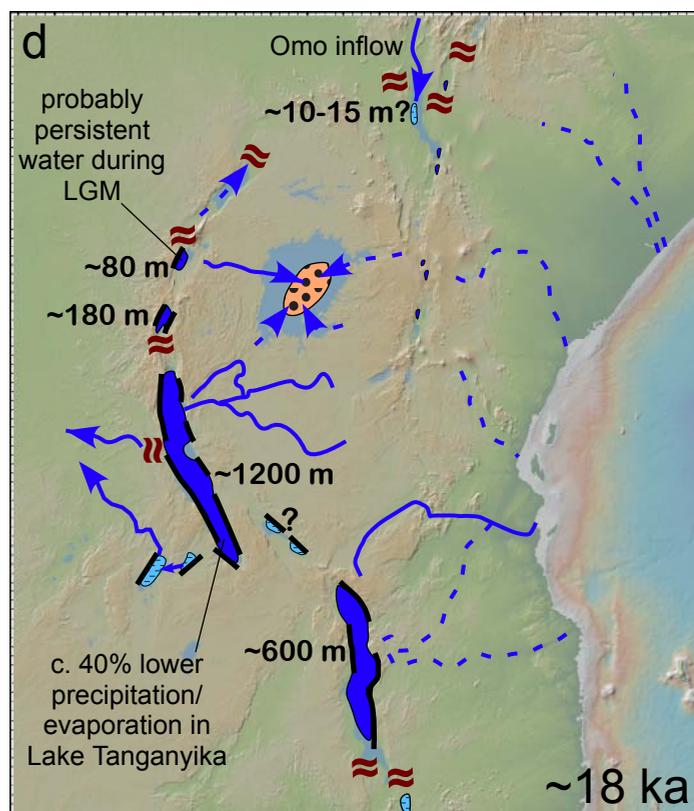
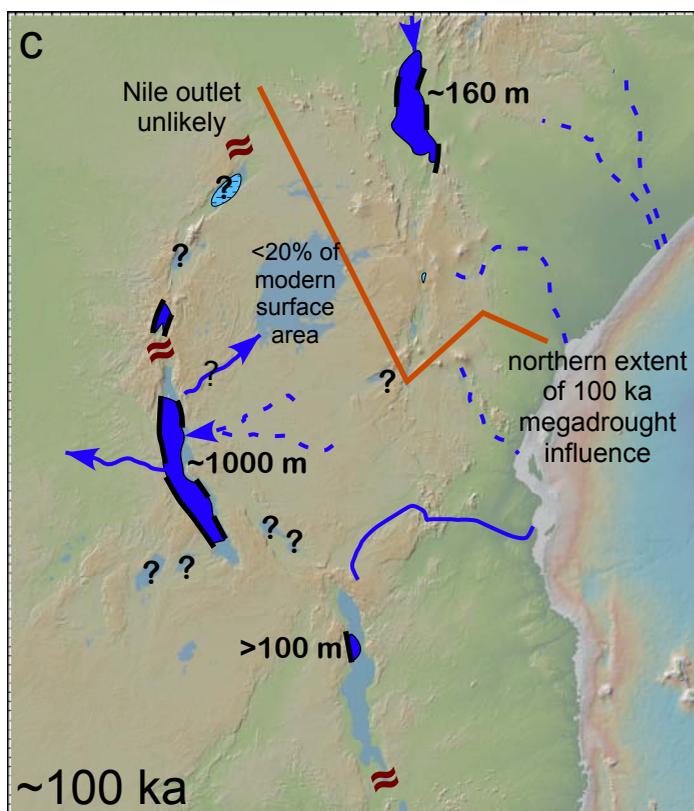
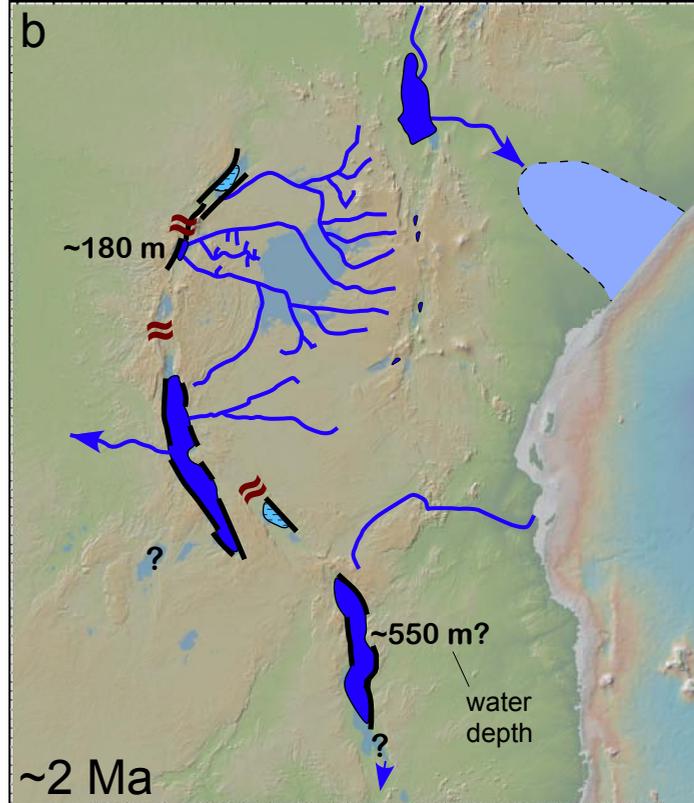
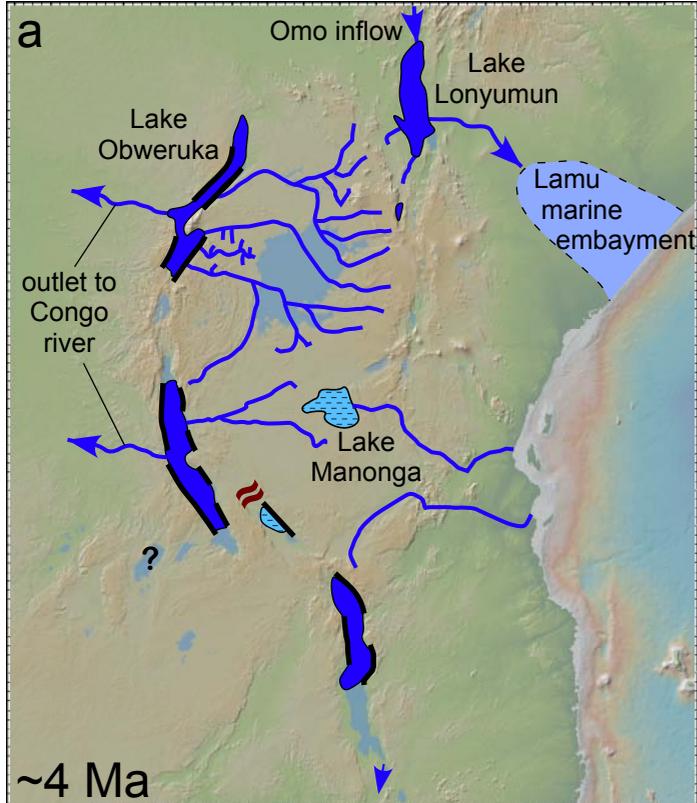




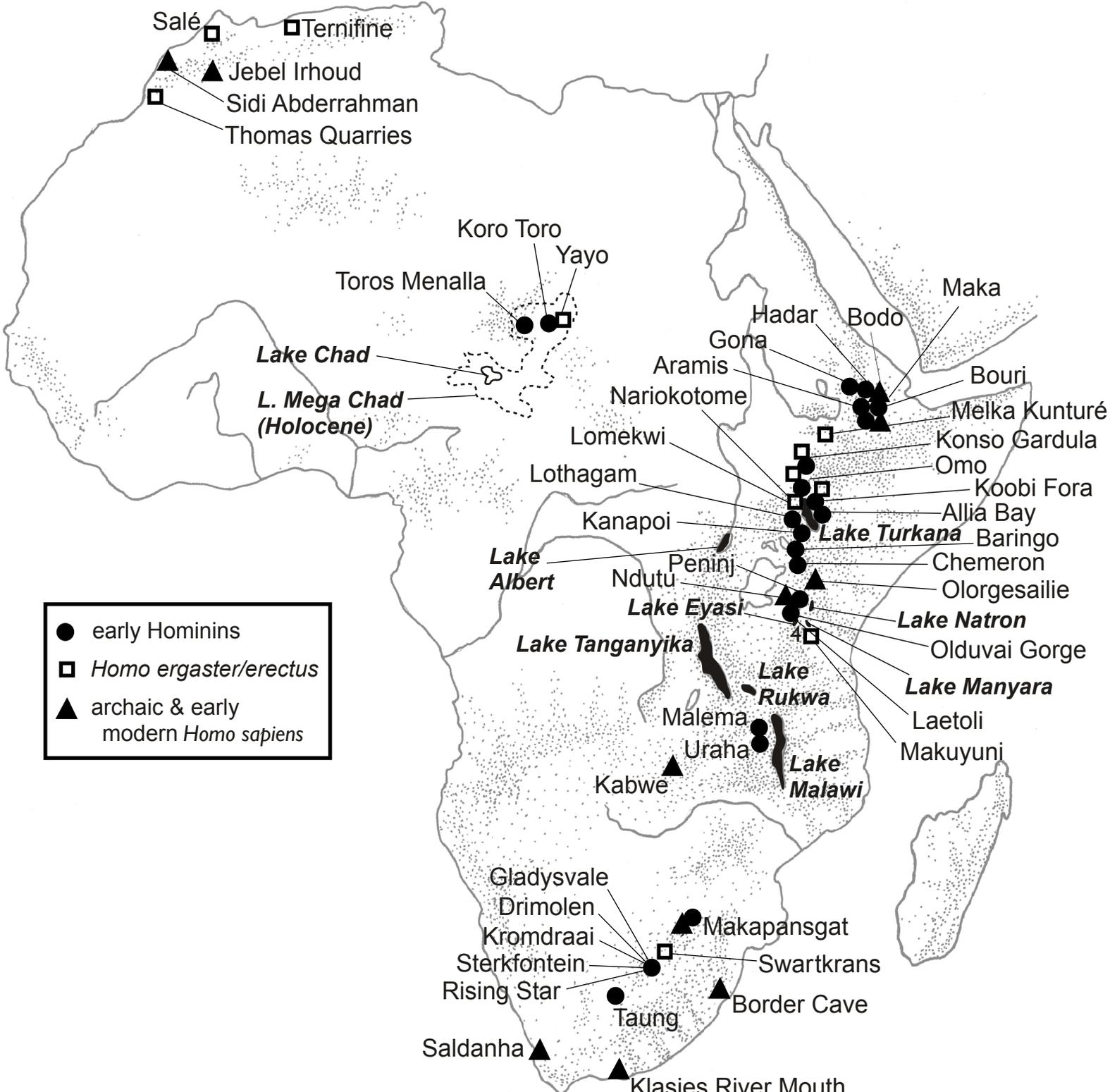








stratified lake
  shallow, holomictic lake
  dry lake
  drainage outlet
  no outlet
  lake margin border fault



Salé  
 Ternifine  
 Jebel Irhoud  
 Sidi Abderrahman  
 Thomas Quarries

Koro Toro  
 Yayo  
 Toros Menalla

Lake Chad  
 L. Mega Chad (Holocene)

Maka  
 Hadar  
 Bodo  
 Gona  
 Aramis  
 Nariokotome  
 Lomekwi  
 Lothagam  
 Kanapoi  
 Lake Albert  
 Ndutu  
 Peninj  
 Lake Eyasi  
 Lake Tanganyika  
 Malema  
 Uraha  
 Kabwe  
 Lake Rukwa  
 Lake Malawi  
 Bouri  
 Melka Kunturé  
 Konso Gardula  
 Omo  
 Koobi Fora  
 Allia Bay  
 Lake Turkana  
 Baringo  
 Chemeron  
 Olorgesailie  
 Lake Natron  
 Olduvai Gorge  
 Lake Manyara  
 Laetoli  
 Makuyuni

- early Hominins
- ◻ *Homo ergaster/erectus*
- ▲ archaic & early modern *Homo sapiens*

Gladysvale  
 Drimolen  
 Kromdraai  
 Sterkfontein  
 Rising Star  
 Taung  
 Saldanha  
 Makapansgat  
 Swartkrans  
 Border Cave  
 Klasies River Mouth