Out of Afar: the first hominin migration. Long-term landscape changes in the Afar region and implications for hominin bipedalism.

Ian G. Smith¶ and Sally C. Reynolds¶

Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Fern Barrow, Poole, Dorset. BH12 5BB

* Corresponding author
Email: ismith1@bournemouth.ac.uk (IGS)

¶These authors contributed equally to this work

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Abstract

Climatic shifts in Africa have long been regarded as a major influence on hominin behavioural adaptations, including the development of bipedalism. The prevailing argument holds that open grasslands favoured the adoption of bipedalism, which can be defined as one of three types: facultative, habitual, and obligate. Across Africa, only one region, Ethiopia, shows evidence of hominins showing all three types of bipedalism: *Ardipithecus* (facultative), followed by *Australopithecus* (habitual), and finally, *Homo* (obligate bipedalism). Was this simply a chance development, a pattern shaped purely by preservation bias, or was there something specific about the Ethiopian region that facilitated the adoption of bipedal behaviours?

This paper introduces the Refugial Bipedalism Model (RBM), proposing that the tectonically complex and relatively isolated Afar region functioned as a long-term evolutionary refugium. We evaluate the unique landscape properties of the Afar region, by reviewing its geological/geomorphological evolution as part of the wider East African Rift System (EARS) and the role it could have played in hominin bipedal locomotion. We suggest that limited carnivoran biodiversity, and lack of migration routes to enter the region may have provided protection (lowered predation and competition) for hominins over millions of years and allowed increasingly upright locomotor behaviours to emerge. The dominance of rifts and cliffs in this tectonically active area might also have facilitated the adoption of new bipedal behaviour that would later prove evolutionarily advantageous.

Around 4.2 Ma, the opening of the Main Ethiopian Rift (MER) enabled southward dispersal, coinciding with the first appearance of facultative bipedal hominins in the Turkana fossil record. Their sudden emergence contrasts with earlier regional absences and may reflect the earliest documented hominin migration “out of Afar” and into wider Africa. By placing the fossil record in a detailed reconstruction of landscape history, this model offers a new explanation for where and when bipedalism first evolved—and why its earliest traces are confined to the Afar region.

1: Introduction

Africa contains a rich record of primates, apes, and hominins stretching back as far as the Oligocene (Stevens et al. 2013; Hammond et al. 2020; Reynolds and Bobe 2022; Urciuoli and Alba 2023). During the Cenozoic, but particularly since the Miocene, Africa's topography has shaped the environments inhabited by our ancestors and the ecosystems of which they were part (Retallack 2001; Moucha and Forte 2011; Cote et al. 2018; Couvreur et al. 2021).

How bipedalism was acquired within the hominins, and the anatomical changes and locomotor patterns that facilitated these behaviours, has been a source of much debate (e.g., Richmond et al. 2001; Pickford et al. 2002; Lovejoy et al. 2009; Lovejoy and McCollum 2010; Haile-Selassie et al. 2012; Daver et al. 2022; Lawrence et al. 2025). However, despite the multiple locomotor hypotheses to explain the hominin behavioural adaptations, the overwhelming consensus is that climatic cooling and drying trends were highly influential (e.g., Vrba 1993; deMenocal 1995; deMenocal 2004; Behrensmeyer 2006). At its simplest, the climate hypothesis suggests that the progressive development of open grasslands favoured the adoption of bipedalism through three not necessarily sequential phases: facultative, habitual, and obligate (e.g., Stamos and Alemseged 2023). We recognise this three-stage framework, *Ardipithecus* as a facultative biped, *Australopithecus* as habitual, and *Homo* as obligate, is a simplified outline of more complex locomotor behaviour, but it does capture a broadly accepted trend in the fossil record.

The challenge here is to understand the type of environment that would favour the early stages of bipedalism (facultative) when adaptation itself would have been nascent, but the risk of predation would have been high. The transition to habitual bipedalism requires arboreal capabilities to be largely abandoned and for the hominin to be able to run to avoid predation. Several alternative ideas have been advanced, in particular the postural feeding hypotheses (Hunt 1996). However, while postural feeding behaviours are common among extant great apes, they lack the kind of selective pressures or environmental challenges that could have led ultimately to sustained terrestrial bipedality.

For some researchers, like Senut et al. (2018), they suggest that a specific type of ecotone, Miombo Woodland, with scattered trees with open ground in between, would have facilitated this transition. However, flora is just one dimension of landscape and the importance of tectonically varied landscapes has been stressed previously as an asset to hominin habitats (e.g., Bailey et al. 2011; Reynolds et al. 2011). Tectonic landscapes provide a diversity of terrains and potable water, as well as cliffs that can provide protection and barriers to other animals and provide conduits for easy movement into adjacent valleys/habitats. Most of these landscapes are associated with the East African Rift System (EARS), which formed around 22-25 million years ago as the Nubian and Somalian plates started splitting apart. The most significant changes have been made in the Ethiopian region, with massive uplift and rifting having transformed this landscape over time, which added to the aridification in the wider region (Sepulchre et al. 2006).

Ethiopia is a region with an abundance of fossil hominins, coupled with many decades of research and publication starting in the 1930s (reviewed in Alemseged 2023). *Australopithecus afarensis* was first found in this region in 1976 and published in 1978 (Johanson 1978). *Ardipithecus* was announced as a separate genus from *Australopithecus* in 1995 (White et al. 1994; White et al. 1995), and then we have the earliest *Homo,* which has been recovered from Ledi-Geraru at 2.8 Ma (Villmoare et al. 2015). This is apart from the existence of *Paranthropus aethiopicus*, discovered in 1968 (Arambourg and Coppens 1967), which is another hominin species, but one not directly ancestral to early *Homo*.

Ethiopia is also one of the few locations where there is evidence of hominins showing all three inferred types of bipedal behaviours: *Ardipithecus* (facultative), followed by *Australopithecus* (habitual), and finally, *Homo* (obligate bipedalism). Hominin bipedalism has also been inferred from the skeletal morphology of the femur in *Ororrin tugenensis*, from Tugen Hills in Kenya (Pickford et al. 2002), and from the *Sahelanthropus tchadensis* hominin individual from Torros Menalla, Chad (Daver et al. 2022). While these claims are widely cited, both identifications remain contentious. In our view, they lack broader contextual support, particularly due to the absence of associated hominin specimens that would indicate an evolving lineage in these regions. Moreover, the environmental reconstructions for both sites suggest relatively stable, forested ecosystems. These conditions, in our assessment, are unlikely to have supported the emergence of obligate or even habitual bipedality, given the selective pressures required to favour such a distinctive and initially disadvantageous mode of locomotion.

While this study does not present new fossil material, the geological and geomorphological synthesis developed here provides a framework for interpreting long-standing gaps and patterns in the hominin fossil record.

Our intention in this paper is not to focus on the hominins and their anatomy, but rather to focus on the landscapes and the impact that these would have had on the evolutionary opportunities for the resident hominins. In a closed environmental system, and given time, evolution will proceed by a series of adaptive experiments. Theoretically, these experiments may survive since closed environments frequently have stable (or reduced) predation, competition, and/or genetic exchange. Survival by fitness pressure may be reduced, thereby aiding evolutionary leaps. In a more open environmental system in which migration is a significant factor, this will act to intensify selective pressures by introducing new predators, along with niche competitors. Closed environments (refugia) may favour radical evolutionary leaps, and potentially speciation, while the opening up of such ecosystems winnows the results of those leaps. We apply this simple evolutionary perspective to the development of hominin bipedalism in relation to the landform development of Afar and Kenya (Fig 1).

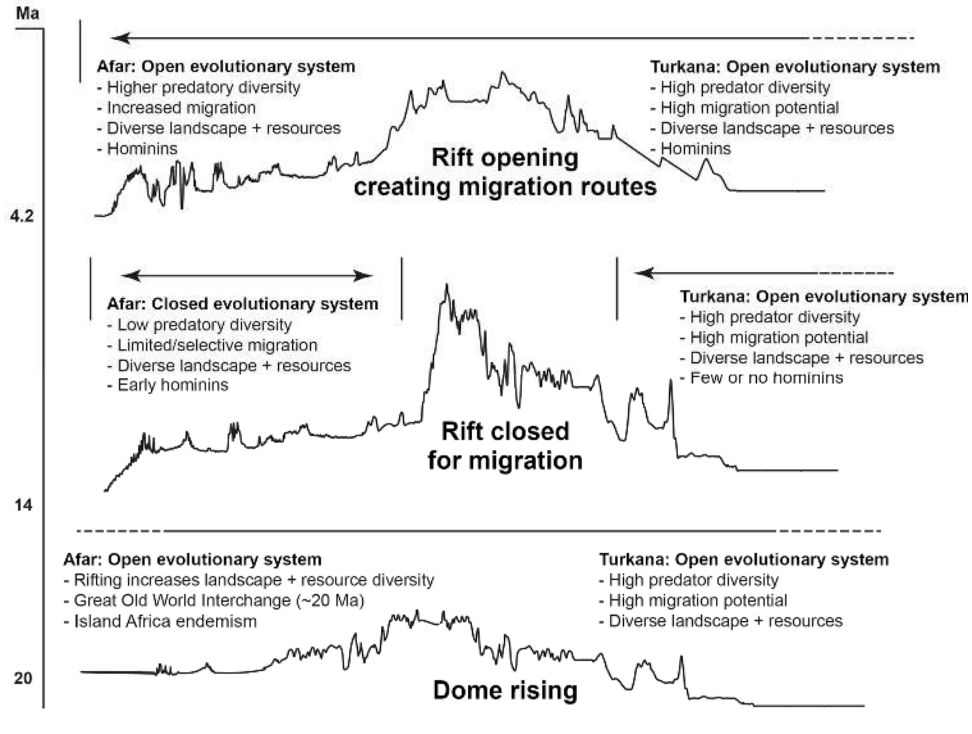

Fig 1. Landform evolution 20 Ma to 4.2 Ma. This conceptual diagram illustrates the temporal stages of landform evolution and how this would have influenced the ecosystems of Afar, compared with the Turkana Basin. In the earliest stages, around 20 million years ago, the rising Ethiopian Dome is not yet able to restrict migration into Turkana from further north. Then, for an extended period of time, this dome, in concert with other landform variables, acts to separate the Afar from the rest of Africa in a closed evolutionary system, which allowed hominin adaptations, such as obligate bipedalism, to occur in a relatively sheltered refugium. Finally, at the top, we see that the opening of the Main Ethiopian Rift after ca. 4.2 million years allows the bipedal hominins to migrate southwards to the Turkana Basin.

Our approach shifts the spotlight from climate or anatomical triggers to long-term geomorphological isolation as a key enabler of behavioural innovation. We suggest that closed landscapes, acting as evolutionary refugia, may have enabled otherwise risky traits like bipedality to emerge and persist before being subjected to selection pressures in more open systems.

Even today, the Ethiopian landscapes possess a high level of endemic species (e.g., Asefa et al. 2020; Demissew et al. 2021) due to their topographic diversity and high levels of tectonic and volcanic activity driven by the rifting of a triple junction (Sani et al. 2017). The thesis here is that this unique landscape evolution in Ethiopia may have created a closed, or semi-closed, environment over millions of years that favoured the development of hominin bipedalism in an ecosystem that provided relative safety. Given that hominin evolution and landscape evolution occur on distinct temporal and spatial scales, we present landform maps of key temporal stages and outline the impact of isolation or migration on ecosystems at each stage. We then discuss the implications of this landform evolution on the subject of hominin locomotion and bipedality.

2: Overview of landform evolution in Africa

2.1: Temporal stage A: Island Africa ca. 110 Ma to ca. 25 Ma

The initial stages are characterised by Afro-Arabia being an isolated landform with no avenues for faunal migration until around 20 million years ago (Fig 2).

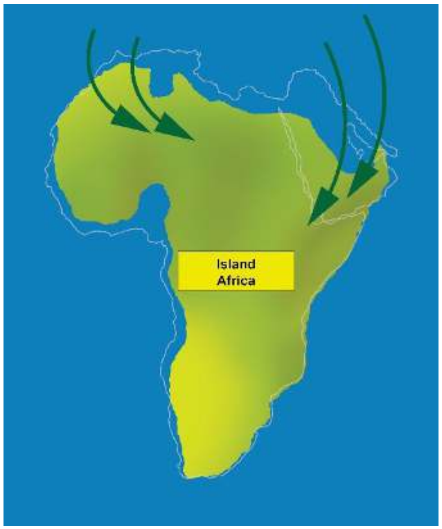

Fig 2. Temporal stage A: Island Africa ca. 110 Ma to ca. 25 Ma. Island Africa, also known as Afro-Arabia, prior to ca. 25 million years ago. Arrows denote migratory phases prior to and leading up to the Great Old-World Biotic Interchange (GOWBI) between Eurasia and Afro-Arabia at around 20 million years ago (redrawn after Seiffert 2012).

The “Island Africa” emerged after separating from South America roughly 110 Ma and, for reasons that are still unclear, exhibited poor species diversity from the outset (Gheerbrant and Rage 2006; Rage and Gheerbrant 2020). There was therefore very little faunal exchange with other continents and this species paucity, and the concomitant growth in endemic taxa, continued until the approaching closure of the Tethys Sea, which finished during the Miocene epoch. Little is known of the fauna inhabiting Africa during this period of isolation, but there was a clade of stem placental mammals, called Afrotheria and are represented by six living placental orders, namely Proboscidea, Sirenia, Hyracoidea, Macroscelidea, Tubulidentata and Tenrecoidea (Stanhope et al. 1998; Sen 2013). The timing of the appearance of this clade is between 74.4 and 96.5 Ma, according to molecular estimates (Meredith et al. 2011), but the fossil record of this time period is poor. From 56 Ma, Island Africa moved closer to Eurasia, at a rate of 2-3 cm per year (McQuarrie et al. 2003; Seiffert 2012), and while these land masses were still isolated, important sweepstakes dispersals took place (rodents, primates, embrithpods and elephantoids to name a few) into Island Africa. The so-called *Gomphotherium* landbridge formed when the two continents finally connected around 20 Ma, initiating a major faunal migration, known as the Great Old World Biotic Interchange (GOWBI) (Sen 2013; Rage and Gheerbrant 2020; Mattingly 2022). Groups of animals that moved from Africa into Europe included proboscideans, hyracoids and tubulidentates (e.g., Sen 2013), while in the opposite direction, the pulses of vertebrate expansion into Afro-Arabia are thought to explain the evolutionary success of many of their descendant species in Africa today (Rage and Gheerbrant 2020).

Molecular divergence rates for primate clades give a Last Common Ancestor (LCA) for crown primates of around 66 million years ago (e.g., Seiffert 2012; Steiper and Seiffert 2012) and therefore suggest that they arrived in Africa from Laurasia (Europe + Asia). By 34 Ma, however, there existed a wide array of primate colonies on the Afro-Arabian continent that experienced multiple competitive phases due to migrations across the Tethys Sea during ‘chance dispersals’ before the GOWBI (Seiffert 2012). These dispersals were primarily into Africa; either via northwest Africa or Arabian routes (Fig 2). The main Paleogene primate-bearing fossil sites in Morocco, Algeria, Libya, Tunisia, Egypt, Saudi Arabia, and Oman imply such possible migratory routes (Gheerbrant and Rage 2006; Seiffert 2012 and references within).

2.2: Temporal stage B: Plume uplift at 32 Ma

This stage sees the incipient formation of the Kenyan and Ethiopian domes. Upwelling in the mantle beneath East Africa started and would eventually create the Ethiopian and Kenyan domes (Rogers 2006). Fig 3 shows a reconstruction of the Afro-Arabian region at roughly 32 Ma.

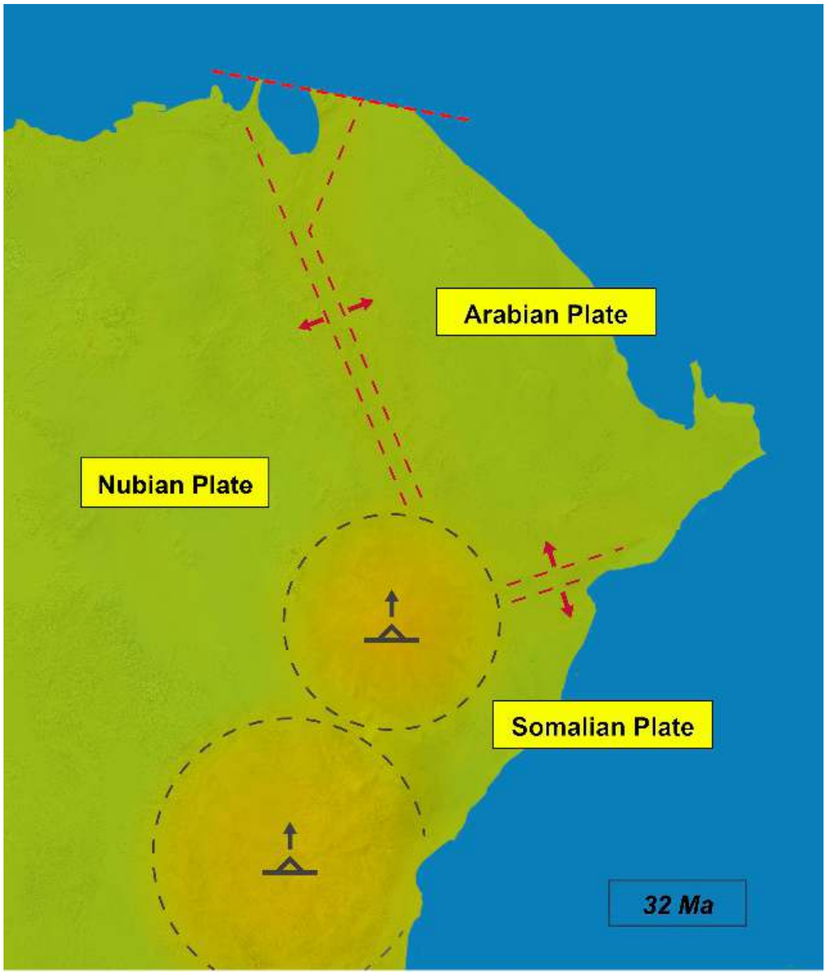

Fig 3. Temporal stage B: Plume uplift at 32 Ma. Reconstructed map of Afro-Arabia as it would have appeared at 32 Mya. The beginning of the Ethiopian and Kenyan domes can be seen (after Rogers 2006). The future major rifting that would lead to the formation of the Red Sea and the Gulf of Aden is clearly marked.

The African Superswell uplifted the majority of the African continent to above 1 km in elevation during this time (Nyblade and Robinson 1994; Lithgow-Bertelloni and Silver 1998). The uplift and erosion initiated at this time have continued since, and Gani and Neupane (2018) suggest that the uplift of the Ethiopian Plateau continues to the present day. This uplift has been implicated in the development of grassland-dominated habitats thereafter (e.g., Sepulchre et al. 2006). Over the past 32 million years, there has been additional mantle plume uplift of between 1 and 2 km (Sembroni et al. 2016a; Xue et al. 2018) supplemented by the deposits of up to 4 km of various volcanic layers (Mohr and Zanettin 1988; Ukstins et al. 2002).

As these landform changes were taking place ca. 32 million years ago, it is reasonable to assume that suitable habitats for primates in Kenya and Ethiopia would largely have resembled key sites from this time period in Egypt, specifically the vertebrate fauna from the site of Birket Qarun Locality 2 BQ-2 (Seiffert et al. 2005a; Seiffert et al. 2005b; Murray et al. 2010; Gentzis et al. 2018). The evidence suggests that this was predominately a freshwater ecosystem, dominated by fish species (e.g. catfish, El-Sayed et al. 2020). The Jebel Qatrani formation (dated to 35.4 and 33.3 million years old in Seiffert 2006) is dominated by aquatic bird species such as the jacana, cranes and the shoe-billed stork (Olson and Rasmussen 1986), but also by primitive prosimians, such as *Wadilemur elegans* (Seiffert et al. 2005b). The fossil avifauna suggests similarities to modern Ugandan swamps bordered by forest and open woodland or grassland. The fish and reptile evidence from Jebel Qatrani indicates that the environment was dominated by catfish and lungfish, which suggests that it was being periodically inundated and desiccated, with spiny-tailed lizards similar to those still living in the area today (Murray 2004; Holmes et al. 2010; Kampouridis et al. 2023).

We propose that this represents the earliest habitat indicator for landscapes that would eventually accommodate hominins like *Ardipithecus* and *Australopithecus*, resembling habitats identified at subsequent hominin sites in Africa, which are distinguished by the presence of freshwater bodies as a vital element. (Vignaud et al. 2002; Reynolds 2007).

2.3: Temporal stage C: Active rifting at 27 Ma

In this temporal phase, Africa moves closer to Europe, and the landscape processes are dominated by the active rifting in regions of the present-day Red Sea and Gulf of Aden (Fig 4), for which onset time estimates vary between 30 Ma (Schettino et al. 2019), while others suggest dates of 24 Ma (Reilinger and McClusky 2011).

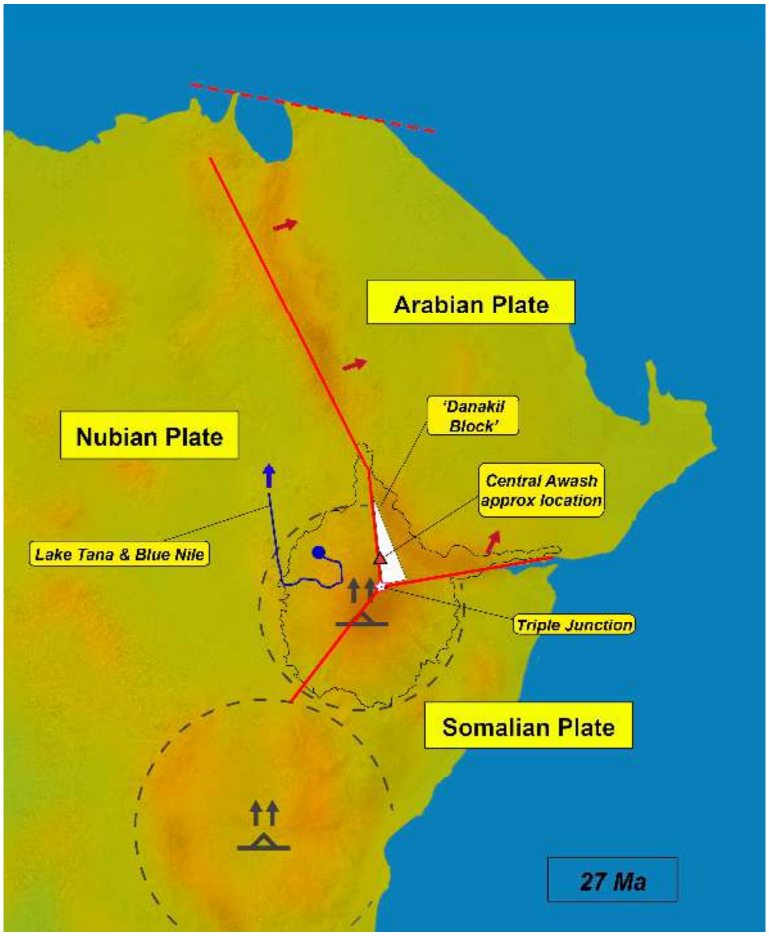

Fig 4. Temporal stage C: Active rifting 27 Ma. Reconstructed map of Afro-Arabia as it would have appeared at 27 Ma. The locations of the Ethiopian and Kenyan plumes (domes) are shown (after Rogers 2006). Rifting (red lines) emanating from the Triple Junction is beginning to partition the Ethiopian Dome to form what will eventually be the Red Sea, the Gulf of Aden, and the Ethiopian Rift Valley. The Afar does not yet exist; neither does the Danakil Block (Schettino et al. 2019). The approximate location of the eventual Central Awash archaeological sites is indicated. The white triangle signifies the area likely to become the Danakil Block. The small white star denotes the approximate Triple Junction location. The eventual locations of Lake Tana and Blue Nile are also shown.

According to Zwaan and colleagues (2019), rifting in the Gulf of Aden began as early as 35 Ma and was followed by oceanic spreading at 17-20 Ma before moving westward towards Afar. Erosion initiated the Blue Nile Canyon (Fig 4), probably as early as 25–29 million years ago (Gani et al. 2007; Sembroni et al. 2016a; Sembroni et al. 2016b), which led to incisions/canyons of up to 1.6 km deep and remains a major source of the River Nile even today. There remains some debate on the northerly route of the river over that timescale (e.g., Gani et al. 2007; Macgregor 2012; Fielding et al. 2018; Abdelsalam 2021).

Habitat conditions at 27 Ma are indicated by sites such as Chilga (1950 masl) to the north of Lake Tana, Ethiopia, which boasts an impressive faunal assemblage that is quite unlike the faunal communities of later time periods in this region. The fauna are dominated by a range of extinct proboscideans, hyracoids and a species of rhinoceros-like embrithopod*, Arsinoitherium giganteum* (Kappelman et al. 2003; Jacobs et al. 2005). The present-day Middle (Central) Awash region (Fig 4) was both inland and in an area dominated by active rifting, as the three plates (Arabian, Nubian and Somalian) are pulled apart. The Red Sea eventually develops to the east of (what will be) the Danakil Block (Fig 4). The Middle Awash region to the west of the Danakil Block would have contained features associated with active rift margins, which include wetlands, cliffs, and heterogenous environments, and would have provided habitat requirements of hominins, namely, sources of fresh water, a range of food resources and a source of predator refuge in the form of cliffs and roosts (e.g., King and Bailey 2006; Bailey et al. 2011; Reynolds et al. 2011).

The Oligocene-Miocene boundary (ca. 23 Ma) is associated with important evolutionary changes where several current lineages of mammalian Orders, including Primates, emerged from sites in the Turkana Basin (Kappelman et al. 2003; Jacobs et al. 2005; Leakey et al. 2011). Multiple sites in the Lake Turkana area have been investigated (Leakey et al. 2011), and Oligocene sites such as Lokone are of a similar age to Chilga (Ethiopia) and Dogali (Eritrea), ca. 26-28 Ma. The Lokone mammals show strong taxic affinities to the material preserved at Fayum in Egypt, yet show less affinities to the younger (Miocene) material in the Turkana Basin or elsewhere in East Africa, which suggests that a later faunal turnover occurred (Leakey et al. 2011). Despite the presence of primates in the Lake Turkana basin, the well-stratified and fossil-rich Nawata formation at Lokone has no hominins before 5 Ma, as indicated by Leakey et al. (2011). Their view being "…it is surprising, and perhaps significant, that hominins are absent until a time close to 5 MYA. Monkeys, on the other hand, are relatively common in the Nawata Formation" (Leakey et al. 2011: 250). We infer that the appearance of hominins soon after 5 Ma might indicate the opening up of a migration route southwards, such as the opening of the Main Ethiopian Rift (MER), which we discuss later.

2.4: Temporal stage D: Danakil plate movements and initiation of Afar Depression at 14 Ma

This temporal stage captures a pivotal tectonic shift—the gradual isolation of the Danakil Microplate from the Nubian Plate, which sets the stage for the eventual formation of the Afar Depression (Fig 5).

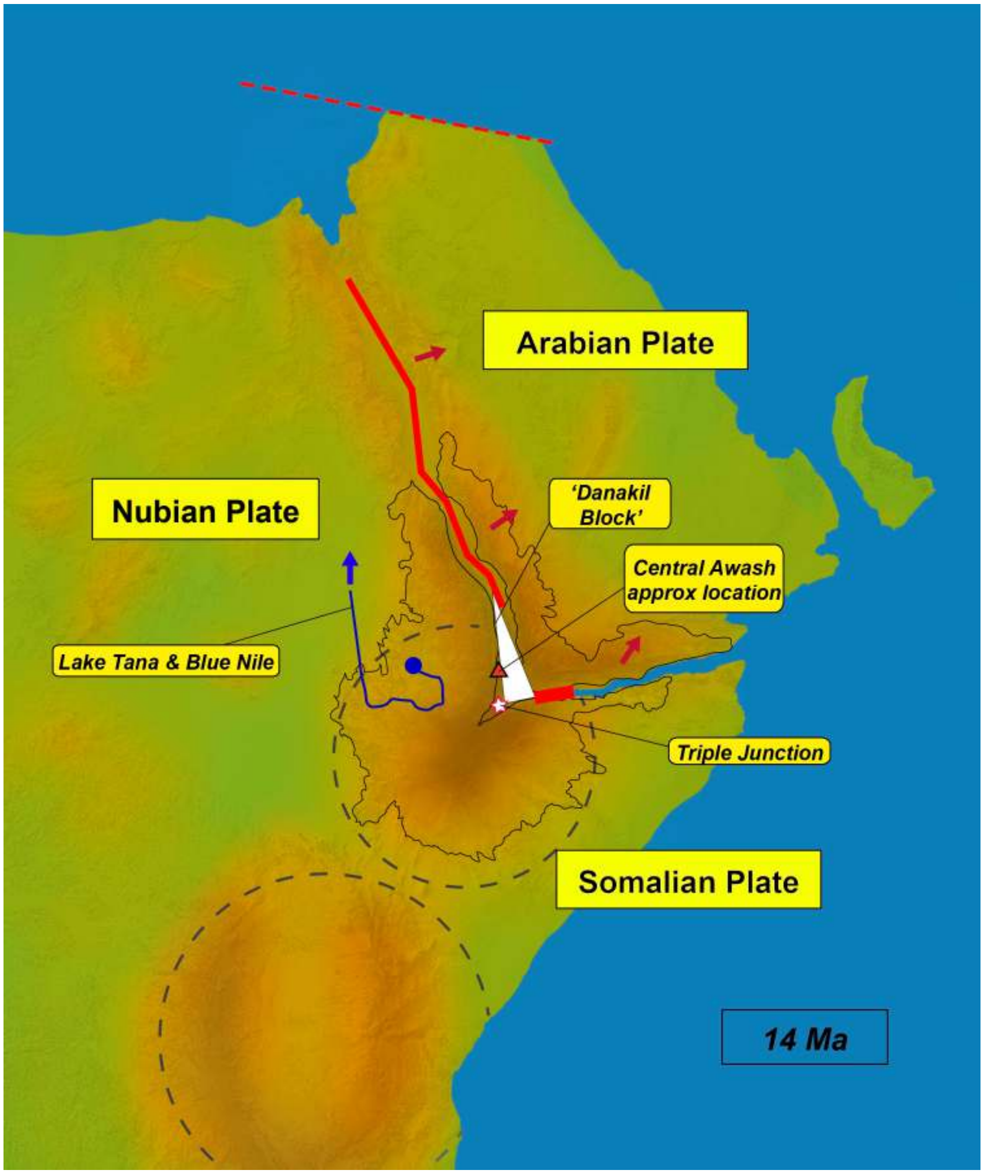

Fig 5. Temporal stage D: Danakil plate movements and initiation of Afar Depression at 14 Ma. Reconstructed map of Afro-Arabia as it would have appeared at 14 Ma. The locations of the Ethiopian and Kenyan plumes (domes) are shown (after Rogers 2006). Continued rifting (red lines) has extended the Gulf of Aden from the Indian Ocean, but the Red Sea has not yet formed. Rifting to the west of the Danakil Block has been replaced by more intense rifting to the east, and soon to become the Red Sea (Schettino et al. 2019). The Afar does not yet exist, but the Danakil Block has started distancing itself from the Nubian Plate. Prior to 14 Ma, the Danakil Microplate is attached to the Nubian Plate, with separation starting from the Arabian Plate at 13 Ma (Reilinger and McClusky 2011; Schettino et al. 2019). The approximate location of the eventual Central Awash archaeological sites is indicated. The white triangle signifies an area likely to become the Danakil Block. The small white star denotes the approximate Triple Junction location. The eventual locations of Lake Tana and Blue Nile are also shown.

Prior to 14 Mya, the Danakil Microplate was attached to the Nubian Plate (described as a ‘close fit’ by Schettino et al. 2019), with the separation from the Nubian Plate possibly starting ca. 13 Mya (Reilinger and McClusky 2011; Schettino et al. 2019), or 11 Mya (Zwaan et al. 2020). This separation of the Danakil Microplate from the Nubian Plate will eventually lead to the formation of, in time, the Afar Depression (Fig 5). Rifting in the Red Sea started at 30 Ma (Schettino et al. 2019) with seafloor spreading in the Central Red Sea and Southern Red Sea dated to around 5 Ma, though it might have started as early as 12 Ma (Zwaan et al. 2019). In the Gulf of Aden, oceanic spreading started at 17.6 Ma (or possibly even 20 Ma in the far east of the Gulf of Aden) and then moved westward towards Afar. Rifting to the west of the Danakil microplate is replaced by intense rifting to the east. The short initial phase of N–S strike-slip fault at 27 Ma between Arabia and Nubia (to the west of the Danakil microplate) was replaced by the development of NW–SE normal faults to the east of the Danakil microplate (Schettino et al. 2019). The net result of these different phases of extensional and strike-slip faulting is the formation of the Afar Depression, and the eventual fusion of the Red Sea with the Gulf of Aden (Schettino et al. 2019).

At this stage, the Danakil Block remains largely intact, but it has begun shifting position relative to both the Nubian and Arabian Plates. The Afar Depression has not yet formed, but the tectonic processes that will eventually create it are now underway. What will become a major topographic low is beginning to take shape, laying the groundwork for a landscape that, in time, will support isolation, endemism, and evolutionary experimentation, key conditions central to the Refugial Bipedalism Model.

2.5: Temporal Stage E: Birth of the Afar Depression at 13-5 Ma

The rotation of the Danakil microplate (Fig 6) was initiated at 13 Ma and was completed by 5 million years ago (Reilinger and McClusky 2011), although Zwaan et al. (2020) suggested a slightly later start for this event at 11 Ma.

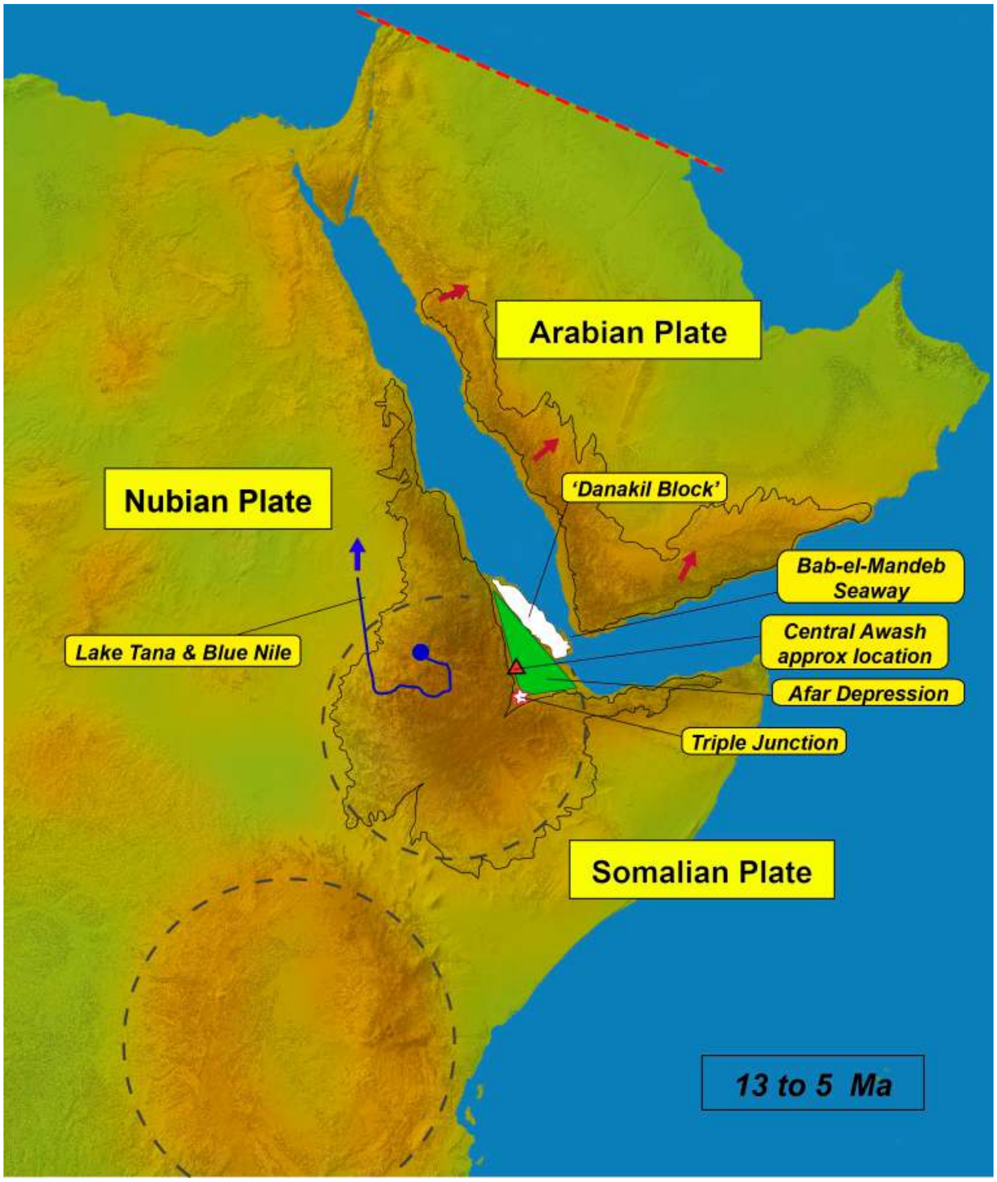

Fig 6. Temporal Stage E: Birth of the Afar Depression at 13-5 Ma. Reconstructed map of Afro-Arabia as it would have appeared ca. 13 to 5 Ma. The locations of the Ethiopian and Kenyan Plumes (Domes) are shown (after Rogers 2006). The rotation of the Danakil Block started at 13 Ma (Reilinger and McClusky 2011) or 11 Ma (Zwaan et al. 2020) and was completed by 5 Ma. The location of the Bab-el-Mandeb seaway land bridge and subsequent Bab-el-Mandeb seaway at 5.3 Ma is shown. The approximate location of the eventual Central Awash archaeological sites is indicated. The small white star denotes the approximate Triple Junction location. The eventual locations of Lake Tana and Blue Nile are also shown.

The formation of the Bab el Mandeb seaway provides the final piece of the puzzle, with the connection of the Red Sea to the Gulf of Aden, and this event sees the Afar region fully isolated from the Arabian Peninsula. Estimates for this event range from 6.2 to 4.5 Ma (Redfield et al. 2003) to 5.3 Ma (Bosworth et al. 2005) when oceanic spreading in the Southern Red Sea initiated an influx of seawater into the Red Sea basin through the Bab-el-Mandeb seaway.

Even prior to the Bab-el-Mandeb seaway incision, the Red Sea basin would have posed a formidable migration barrier to species. There has been a continual process of sea influx followed by water evaporation over the period 12–5 million years ago prior to this, making the environment one of extensive evaporite deposition (Orszag-Sperber et al. 2001; Bosworth et al. 2005; Fernandes et al. 2006), which would be a challenging area to cross for many species. There was little likelihood of species (such as primates) making such a crossing between 12–5 Ma.

The existence of a land bridge between Afar and the Arabian Peninsula during this period explains the closely related taxa and species migrations between the Horn of Africa and Arabia in the Miocene (Redfield et al. 2003; Stewart and Murray 2017 and references therein; Grossman et al. 2019). Examples include various freshwater fish, gecko, monitor lizard, terrapin, extinct elephants, vipers and cobras. Studies of the late Miocene Baynunah Formation, Abu Dhabi, exposed a 6.5 to 8.0 Ma fossil guenon that represents the earliest cercopithecine (and only guenon) yet known outside of Africa (Gilbert et al. 2014; Gilbert and Hill 2022). The dispersal scenarios for cercopithecoid primates out of Africa and through Arabia suggest that the land bridge was a probable route into Asia. There is much speculation about where hominins originated (Africa, Asia or even Europe), but we concur with Harrison (2010) that hominins likely arose in Africa.

At around 5.3 Ma, the Bab-el-Mandeb land bridge disappears, and the whole Afar Depression and the Central Awash area within would have become isolated (Redfield et al. 2003). The depression is bounded by steep, uplifted, rift flanks to the south and to the west, and by the Danakil Block and the Red Sea to the east (Fig 6). To the North lies the Levantine corridor, which is the only migration corridor between Africa and Eurasia (e.g., Grossman et al. 2019). By this time, the Central Awash region had been located in a region of active rifting for upwards of 25 million years. The rifting would have increased the region’s geographic isolation, which was made even greater by the opening of the Bab-el-Mandeb seaway.

The first hominins enter our story at this point with *Ardipithecus kadabba* appearing in the fossil record at around 6.3 Ma, with the descendant species *Ardipithecus ramidus* appearing at 4.4 Ma (White et al. 1994; White et al. 2009; Simpson et al. 2015). The habitats associated with these hominins appear to be largely wooded in character. Overall, the species most commonly recovered with *Ardipithecus ramidus* are generally other species of smaller monkeys and tragelaphin antelopes, which together suggest a wooded environment. The relatively low numbers of recovered carnivore species are of particular interest in the Awash region, as these were the potential predators of hominins and other medium-sized mammals. The Awash region between 13-5 Ma includes only two genera of sabre-toothed cats, namely *Dinofelis* and *Machairodus*, two hyaenids (*Ikelohyaena abronia* and cf. *Crocuta* cf. *dietrichi*), as well as the ursid genus *Agriotherium* and the canid genus *Eucyon* (Louchart et al. 2009). There are signs that the fossil remains associated with the *Ardipithecus ramidus* assemblage were carnivore-ravaged but with a relatively modest number of carnivore species represented (Louchart et al. 2009; White et al. 2009). This is in stark contrast to the larger numbers of predators at later hominin sites, such as Pliocene Sterkfontein (O'Regan and Reynolds 2009). The majority of the carnivoran guild at that time was composed of small viverrids and aquatic fauna, such as otters, which would not typically have preyed on *Ardipithecus*-sized mammals; the adult estimates for this are about 50 kg (Haile-Selassie and WoldeGabriel 2009; White et al. 2009).

The thesis here is that the active tectonic faulting of the region and its isolation from Arabia and the rest of Africa, due to the Ethiopian Dome, may have provided a closed environment in which evolutionary experiments such as *Ardipithecus* could have taken place. The reduced carnivore diversity likely reflected this closed and isolated environment.

2.6: Temporal stage F: Formation of the MER at ca. 5 Ma

This stage sees the Main Ethiopian Rift (MER) eventually open to allow faunal migration to the south. In the period leading up to 5 Ma, the region experienced continued mantle plume activity, which would have likely uplifted the Ethiopian plateau further (Gani et al. 2007). Given the varied tectonic timings/activities and the underlying lithospheric properties, the Main Ethiopian Rift (MER) is often viewed as 3 distinct sections: the Northern MER, the Central MER and the Southern MER (Fig 7).

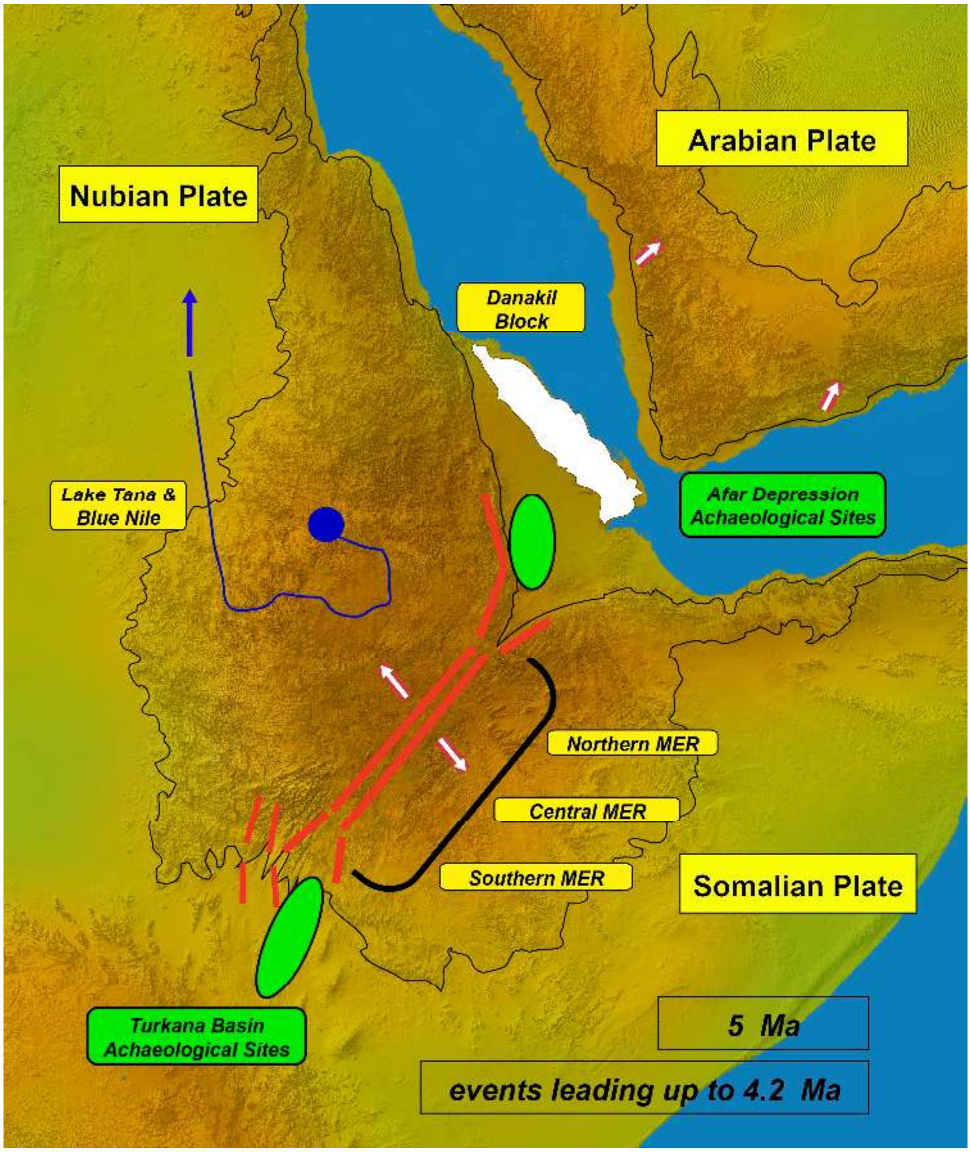

Fig 7. Temporal stage F: Formation of the MER at ca. 5 Ma. Reconstructed map of Afro-Arabia as it would have appeared around 5 million years ago. The Main Ethiopian Rift (MER) is composed of Southern, Central, and Northern sections. Hominin fossil sites are present in the Afar Depression at 5 Ma, but crucially, none have been found from the Turkana Basin until ca. 4.2 Ma; after the opening of the MER.

As such, explanations concerning the opening of the MER involve detailed consideration of each (Bonini et al. 2005; Abebe et al. 2010; Corti et al. 2013; Keir et al. 2015). There are varied interpretations on events and their timings, though Keir et al. (2015) and Abebe et al. (2010) suggest the Central MER was the last section to experience rifting and therefore the step that eventually allowed the opening of the MER (indicated in Fig 7). The exact estimates for the date of this event differ with authors; suggesting younger than 8 Ma ago (Abebe et al. 2010), between 5-6 Ma (Bonini et al. 2005), 5.2 Ma (Gani et al. 2007), and around 5 Ma (Macgregor 2015). While future fossil discoveries or revised chronologies may eventually extend the timing of hominin dispersal slightly earlier than 4.2 Ma, this horizon currently marks the earliest unambiguous evidence of bipedal hominins outside Afar.

3: The enigma of the Mursi Formation

The period prior to 4 Ma is important in hominin evolution, marking the transition from *Ardipithecus* to *Australopithecus*. If the former is indeed a direct ancestor of the latter, then a rapid speciation event likely occurred from 4.4 Ma to 4.2 Ma (Drapeau et al. 2014). The Mursi Formation in the Omo Valley spans this period and offers one of our best opportunities for analysis. This important site region falls outside of the Afar Ethiopian region and to the south of the Main Ethiopian Rift (MER) (Fig 8). Chronological estimates for the Mursi Formation vary: 4.05 to 4.25 Ma (Butzer and Thurber 1969), greater than 4 Ma (Drapeau et al. 2014), 4.0 to 4.5 Ma (Coppens 1978), and 4.5 Ma as the start of the Mursi Formation's sedimentation (Brown and de Heinzelin 1983). A reasonable consensus places the formation therefore between 4.0 and 4.5 Ma.

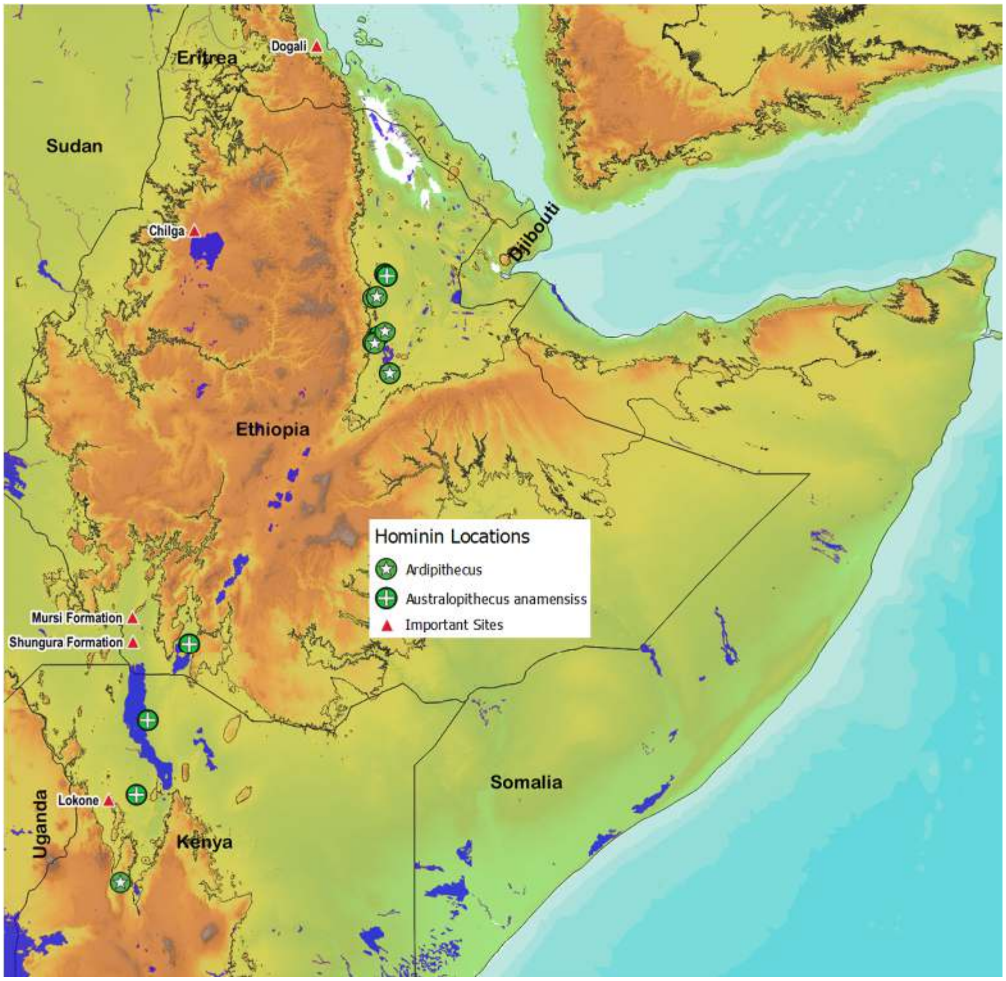

Fig 8. Major hominin and formation sites in Omo-Turkana Basin and Afar Depression. Present-day topographic map of East Africa showing locations of *Ardipithecus* and *Australopithecus anamensis* fossil sites, formation sites and paleoenvironment sites mentioned in the text.

Drapeau et al. (2014) reported 250 fossil specimens from Mursi; yet unexpectedly, no primates and, in particular, no hominins were identified. Given the abundance of hominin fossils in nearby areas of the Omo-Turkana Basin, this absence is striking. In contrast, *Australopithecus anamensis*, the oldest known hominin in the basin, is present at Kanapoi (4.2–4.1 Ma) and Allia Bay (3.97 Ma) (Fig 8), and the paleoenvironments of those sites are well understood (Bobe et al. 2020; Frost et al. 2020; Manthi et al. 2020; Dumouchel et al. 2021).

To understand why *Australopithecus anamensis* appears at Kanapoi and Allia Bay but not at Mursi, Dumouchel (2018) conducted a comparative analysis of the three fossil localities. The prevailing explanation is that *A. anamensis* was more common in relatively open, seasonally dry habitats and absent in more humid or closed settings. Beasley (2016) offered an alternative interpretation, suggesting the absence of hominins at Mursi may result from sampling limitations.

Dumouchel and Drapeau (2014) conducted yet further research with taphonomic analyses of the fossil fauna from the Mursi Formation and Member A of the Shungura Formation. They concluded that both environments are remarkably similar (Fig 8). Yet despite this, no hominins have been recovered from the Mursi Formation. The age ranges are also broadly consistent; the Mursi Formation spans 4.0 to 4.5 Ma and underlies the Shungura Formations (3.59-3.33 Ma), with Dumouchel and Drapeau concluding that fossils found within the Mursi Formation are indeed contemporaneous with those found in Member A of the Shungura Formation.

We suggest that the first appearance of hominins in the later time period might not reflect climatic differences, but rather the opening of the southward dispersal corridor along the MER. If this is the case, the Mursi Formation represents a viable habitat that remained unoccupied simply because it lay beyond the dispersal range of early bipedal hominins evolving in isolation farther north.

These observations suggest that the absence of hominin fossils in southern Ethiopia and Kenya prior to ca. 4.2 Ma reflects a genuine biogeographic boundary rather than sampling bias. To reinforce this pattern, Table 1 summarizes known occurrences of fossil apes and early hominins across Ethiopia, Kenya, and Tanzania. The data illustrate a clear temporal and regional discontinuity, with Kenya and Tanzania hosting a rich record of Miocene apes but no confirmed hominins until after the likely opening of the Main Ethiopian Rift.

APE AND HOMININ SPECIES	AGE (MILLION YEARS AGO)	ETHIOPIA	KENYA	TANZANIA
HOMO SAPIENS (EARLY)	>160 ka	Omo Kibish, Herto (Middle Awash)	Widespread	Widespread
HOMO ERECTUS / H. ERGASTER	1.8 - 0.8 Ma	Melka Kunture, Konso	Widespread	Widespread
HOMO HABILIS (FRAGMENTARY)	2.4 - 1.4 Ma	Gona and Omo (tentative)	Yes - Koobi Fora	Yes, Olduvai Gorge
AUSTRALOPITHECUS GARHI	2.5 Ma	Bouri, Middle Awash	Not Found	Not Found
AUSTRALOPITHECUS DEYIREMEDA	3.5 - 3.3 Ma	Woranso-Mille	Not Found	Not Found
AUSTRALOPITHECUS AFARENSIS	3.9 - 3.0 Ma	Hadar, Dikika	Yes	Yes
AUSTRALOPITHECUS ANAMENSIS	4.2 - 3.9 Ma	Asa Issie, Middle Awash	Kanapoi	Not Found
ARDIPITHECUS RAMIDUS	4.4 Ma	Aramis, Afar Depression	Not Found	Not Found
ARDIPITHECUS KADABBA	5.8 - 5.2 Ma	Middle Awash	Not Found	Not Found
CHORORAPITHECUS ABYSSINICUS	~8 Ma	Chorora Formation	Not Found	Not Found
SAMBURUPITHECUS KIPTALAMI	9.5 Ma	Not Found	Samburu Hills	Not Found
KENYAPITHECUS WICKERI	14 Ma	Not Found	Fort Ternan	Not Found
NACHOLAPITHECUS KERIOI	15 Ma	Not Found	Nachola (Northern Kenya)	Not Found
EQUATORIUS AFRICANUS	15.5 - 15 Ma	Not Found	Cheboit and Tugen Hills	Not Found
AFROPITHECUS TURKANENSIS	17 - 16 Ma	Not Found	Kalodirr (Lake Turkana Basin)	Not Found
TURKANAPITHECUS KALAKOLENSIS	17 - 16 Ma	Not Found	Kalodirr (Lake Turkana Basin)	Not Found
PROCONSUL MAJOR	18 Ma	Not Found	Mfangano Island	Not Found
PROCONSUL HESELONI	18 - 17 Ma	Not Found	Koru, Songhor	Not Found
NYANZAPITHECUS VANCOUVERINGORUM	18 - 17 Ma	Not Found	Songhor	Not Found
NYANZAPITHECUS PICKFORDI	18 - 17 Ma	Not Found	Songhor	Not Found
PROCONSUL NYANZAE	19 - 18 Ma	Not Found	Songhor	Not Found
PROCONSUL AFRICANUS	20 - 18 Ma	Not Found	Rusinga Island	Not Found
RUKWAPITHECUS FLEAGLEI	~25 Ma	Not Found	Not Found	Rukwa Rift Basin
NSUNGWEPITHECUS GUNNELLI	~25 Ma	Not Found	Not Found	Rukwa Rift Basin

Table 1. Distribution of selected Miocene ape and early hominin fossils in Ethiopia, Kenya, and Tanzania. Kenya and Tanzania preserve numerous Miocene ape species but lack evidence for early bipedal hominins before ca. 4.2 ma. In contrast, Ethiopia—particularly the afar region—shows a sequence from facultative to obligate bipedality, consistent with its role as an evolutionary refugium.

4: Turkana Basin

Between 5 Ma and 3 Ma, the Turkana, Omo and Chew Bahir rifts entered their main subsidence/sedimentation phase in the Omo-Turkana Basin (Feibel and Schwindinger 2011, 2012; Macgregor 2015). This progressive rifting and opening of basins to the south after ca. 4.2 Ma essentially displaced the ecosystem to the south, progressively reducing regional isolation and shifting the landscape toward a more open system in which predation could occur more intensively.

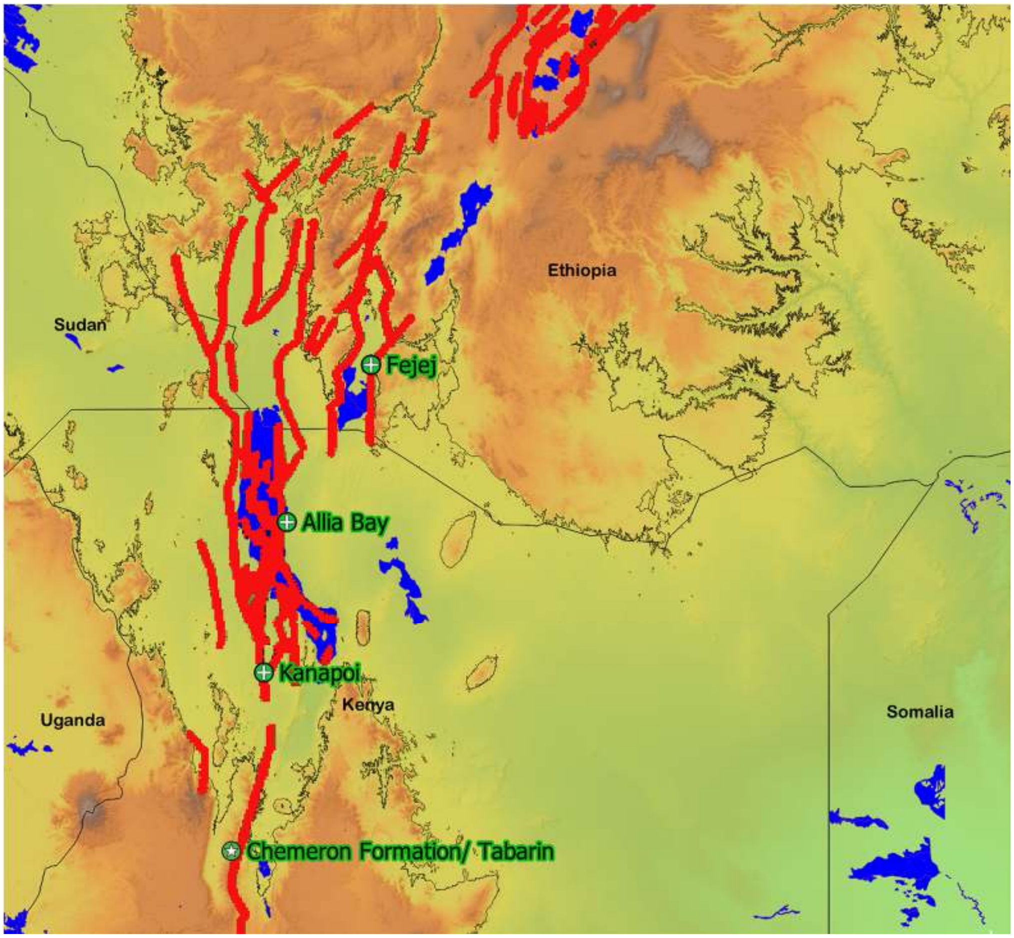

Fig 9. Proximity of *Australopithecus anamensis* sites to rifting process. Showing the rifts in the Omo-Turkana area at 5 Ma (Macgregor 2015) superimposed on the present-day topographic map of the Turkana Basin. Shows the four major *Australopithecus anamensis* sites of Fejej, Allia Bay, Kanapoi and Chemeron Formation at Tabarin all lie on major rifts.

Between 5 Ma and 4 Ma, the Turkana Basin was a dynamic environment that alternated between fluvial, deltaic, and lacustrine settings due to shifting flows of the Omo, Turkwell, and Kerio rivers. At 4.5 Ma, these ancient rivers created the "phantom" Turkana River in the Apak Plain, which flowed into the Indian Ocean in the southeast (Feibel and Schwindinger 2011, 2012). The Omo-Turkana basin filled with paleo-lake Lonyumun about 4.14 Ma, pushing trees and grasslands to the basin's borders (Feibel and Schwindinger 2011, 2012; Bobe et al. 2020; Manthi et al. 2020). As Fig 9 demonstrates, at 5 Ma a passage along the cliffs/escarpment from the MER could have enabled hominin movement towards Fejej, Allia Bay, Kanapoi and Chemeron Formation at Tabarin. These locations lend support to the idea that these geological rift structures facilitated hominin migration.

Once hominins dispersed from the MER and into southern Ethiopia and Kenya, they encountered new selective pressures. In this more competitive landscape, marked by a complete carnivore guild and open savannahs, natural selection would have favoured those individuals more adept at bipedality and predator avoidance. This increased pressure would have further refined bipedalism, reinforcing it not merely as a tolerated behavioural strategy, but as an adaptive advantage.

While a few southerly sites have yielded fragmentary remains that some have interpreted as early hominins, most notably the Lothagam mandible (KNM-LT 329) and the Tabarin mandible (KNM-TH 13150), these specimens do remain taxonomically uncertain, as are their dates (Kissel and Hawks 2015). We therefore treat them as possible, but unconfirmed, early hominins that do not necessarily contradict the broader pattern of secure bipedal hominin fossils appearing outside Afar only after approximately 4.2 Ma.

5: Bipedalism and climate change

The process of adopting habitual bipedal behaviours would have been a dangerous and complex experiment for any hominin living within typical African ecosystems, where numerous predators were present. Yet Thorpe et al. (2014) suggest that some level of facultative bipedalism is remarkably common among primates and may arise quite naturally, and the fossil record supports this view. There are other genera of bipedal apes that evolved in various places around the world.

The Miocene ape *Oreopithecus* represents one such case, having evolved terrestrial bipedality in the swampy forested islands of the Tusco-Sardinian region, likely facilitated by an absence of natural predators. (Rook et al. 1999; Hammond et al. 2020). This Late Miocene great ape inhabited Tuscany and Sardinia in Italy, which at that time were isolated from the European mainland (Sartori 2001; Rook et al. 2006a; Rook et al. 2006b) forming a distinctive faunal environment, the so-called

Tusco-Sardinian palaeobioprovince. Oreopithecus exhibits a range of anatomical features that successive authors have described as “unique” or even “bizarre,” likely shaped by evolution under insular conditions (Köhler and Moyà-Solà 1997). Around 6.7 Ma, climate change and renewed connection to the mainland ended this insular phase. The influx of new fauna, including predators, likely contributed to the extinction of Oreopithecus (DeMiguel and Rook 2018).

Various theories have been proposed over recent decades to explain a direct link between human/mammalian evolution and climate/aridity, such as pulsed turnover hypothesis (Vrba 1993), aridity hypothesis (deMenocal 1995; deMenocal 2004), variability selection hypothesis (Potts 1998), and the pulsed climate variability hypothesis (Maslin et al. 2014). However, these ideas have been increasingly called into question. McKee (2017) argues that hominin bipedality predates the much-heralded climatic changes in the various climate theories, so other factors must have been responsible for this momentous hominin evolutionary step. He explains the process of hominin bipedalism as being autocatalytic, driven by self-generating feedback loops where one evolutionary step is a sufficient catalyst for the next, irrespective of changes in the external environment. Maxwell et al. (2018) similarly conclude that any apparent links between early hominin diversity and indications of climate instability are likely caused by the differences in rock exposure and collection effort.

These critiques align with the view presented in this paper: that tectonic and topographic isolation, rather than aridity or climate variability, created conditions in which risky traits like bipedalism could first emerge. Our Refugial Bipedalism Model builds on this perspective by emphasising the role of geomorphological refugia in enabling evolutionary experimentation, followed by selective filtering once dispersal corridors opened.

6: Discussion

In brief, the above geological review suggests that the Afar region was at first open. Each stage of the isolation and opening of the region offered evolutionary opportunities to hominins experimenting with bipedal behaviours. The tectonic rifted landscapes provided a barrier to migration, and the evolutionary consequences of this are the high numbers of new mammal species identified in the Miocene Middle Awash deposits (Vrba and Haile-Selassie 2006), as well as high levels of endemism today in rodents and other mammals (Yalden and Largen 1992; Tefera 2011; Bryja et al. 2022), reptiles and fish (Wagner et al. 2013; Stewart and Murray 2017), and also in plant species (e.g., Friis et al. 2005; Wang et al. 2020).

Our primary focus is on the importance of a prolonged refugial phase in Afar in shaping hominin evolution, specifically as a closed or partially closed ecosystem, at least for medium-sized and small mammals. The fossil record for this time indicates a reduced number of predators, and the lack of migration would have reduced niche competition. The emergence of facultative bipedal hominins and ultimately habitual bipeds occurred in this uniquely protected ecosystem. Though geographically constrained, Afar was likely ecologically varied. Rift activity and hydrology would have created a patchwork of habitats, offering hominins niche flexibility and routes for predator avoidance. Research in the Plio-Pleistocene Baza Basin of southern Spain shows that tectonic and hydrothermal processes created persistent wetland microrefugia that supported diverse mammal communities (García-Aguilar et al. 2024). Similar mechanisms may have operated in Afar, producing localised ecological buffers that helped early hominins avoid predation and exploit varied niches.

As the East African Rift opened southward, creating a route through the Ethiopian Plateau, this system transitioned into a more open ecosystem in which migration, competition and predation pressures increased. Joordens et al. (2019) have highlighted the possible importance of a coastal refugium in possibly explaining movements southwards, but here our focus is on the inland migration routes via the MER.

The rapid diversification of the australopithecines following the opening of this gateway south was likely driven by increased evolutionary pressures, in which some of the ‘Afar experiments’ survived while others did not. In our model, hominin bipedality is understood as a function of landscape, where barriers to migration created evolutionary space for risky traits to emerge and stabilise. We also propose that the relative isolation of Afar may have amplified the effects of genetic drift. In small or semi-isolated populations, novel traits, including early forms of bipedality, can become fixed even without strong directional selection. This process, operating alongside reduced predation and ecological opportunity, may have helped consolidate bipedal behaviours before they were subjected to harsher filtering in more competitive or open environments.

The unique nature of the Afar region has been widely recognised before, with some authors referring to it as a refugium, which is not new, despite it being a vast region covering ca. 100,000 square kilometres and with geomorphology that has been constantly changing over the past 30 million years. The concept of ‘refugia-within-refugia’ (see Abellán and Svenning 2014) or ‘microrefugia’ (Hylander et al. 2015) may help visualise how processes of endemism and speciation occurred at highly localised scales.

We suggest that the constant volcanics/rifting is pushing the refugial environment to the next valley and allowing hominins to follow, possibly via cliff conduits. This is not dissimilar to the complex topography hypothesis (Winder et al. 2013; Winder et al. 2015), where it is suggested hominins developed substantial reliance on bipedalism from scrambling across/up/down hills and rock faces generated from the tectonic and rifting processes around it. The Hadar and Busidima Formations Tuffs suggest highly localised “basin-scale geological processes” in Afar (Roman et al. 2008); which further supports the idea of micro-scale refugia. Dikika, Gona, Hadar, and Ledi-Geraru are only a few km apart, and whereas the sites are now on uplifted locations away from the active volcanism, they were once located near the rift valley floor (King and Bailey 2006), providing a confined setting for hominin innovation.

7: Conclusion

These traits, we argue, have allowed evolution to proceed in a largely closed environment, which ultimately became an open environment, which allowed the hominins to migrate south. The preservation record of the African hominins and their adaptations appears to support the notion that bipedalism was widespread across both closed and open habitats (for *Ardipithecus* versus *Orrorin* and *Sahelanthropus*, respectively). Miocene ape bipedalism is not even an exclusively African phenomenon, with *Oreopithecus bambolii* also a well-known example of a bipedal, insular, hominoid species (Rook et al. 1999).

This Refugial Bipedalism Model (RBM) places less emphasis on climate change as a key factor in hominin evolution, which is at variance with a great deal of previous work on the subject (Bobe et al. 2002; Behrensmeyer 2006; Bonnefille 2010; deMenocal 2011; Maslin et al. 2014; Gilbert and Hill 2022). Specifically, we focus on the Ethiopian region as a region of interest, as it is the only African region with evidence of successive phases of bipedalism, namely facultative, habitual, and finally obligate bipedalism (Stamos and Alemseged 2023). Within this region, we have identified that the opening of the Main Ethiopian Rift (MER), which started at around 5 million years ago, allowed well-adapted facultative hominins out of the Afar refugial area to finally migrate southwards into Kenya, where they subsequently appear in the fossil record of the Turkana Basin (Bonini et al. 2005; Abebe et al. 2010; Corti et al. 2013; Keir et al. 2015).

Previous studies have highlighted the important contrasts in the role of the African regions of eastern versus southern Africa, where eastern Africa appears to be an important centre of speciation and endemism while southern Africa preserved this biodiversity (Reynolds 2007). Now, it appears that the regions within East Africa were also playing subtly different roles. Recent palaeobiotic research shows that regional mammal communities across the East African Rift were much more distinct during the late Miocene and early Pliocene, only becoming homogenised after ca. 3 Ma (Rowan et al. 2024). This pattern of early endemism aligns with our hypothesis that Afar functioned as an ecological refugium, permitting evolutionary divergence in relative isolation.

Ongoing research is integrating palaeontological data on vertebrates, primates, and hominins across successive time periods in these regions to further investigate these emerging patterns. Our findings suggest that it was the dynamic interplay between climate, landform evolution, and tectonic processes that created the unique environmental conditions necessary for the successful emergence and consolidation of bipedalism.

Rather than dismissing climate-based or anatomical models, the Refugial Bipedalism Model provides a clearer explanation of how and why early bipedality emerged where it did. By emphasizing the evolutionary impact of tectonic isolation, it helps address fossil distribution patterns that remain challenging for existing frameworks to explain. Geomorphological complexity may have enabled repeated cycles of isolation and re-connection that shaped hominin adaptation in ways underappreciated in current models. We acknowledge that some may view this hypothesis with caution given the patchiness of the fossil record, but our aim is to provoke constructive engagement by offering a geologically informed perspective that could integrate behaviour, ecology, and landscape history and thus enhance our overall understanding. As more fossil data and geomorphic reconstructions become available, the RBM can be further refined and tested. If borne out, it may hold broader implications for understanding how topographic refugia function as cradles of evolutionary innovation.

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9: Author Contributions Statement

Conceptualization: Ian G. Smith
Methodology: Ian G. Smith
Software: Ian G. Smith
Validation: Ian G. Smith, Sally C. Reynolds
Formal analysis: Ian G. Smith, Sally C. Reynolds
Investigation: Ian G. Smith, Sally C. Reynolds
Resources: Sally C. Reynolds
Data curation: Ian G. Smith, Sally C. Reynolds
Writing – original draft: Ian G. Smith
Writing – review & editing: Ian G. Smith, Sally C. Reynolds
Visualization: Ian G. Smith, Sally C. Reynolds
Supervision: Sally C. Reynolds
Project administration: Sally C. Reynolds
Funding acquisition: Sally C. Reynolds

10: References

Abdelsalam, M. G., 2021. The Young Nile. *Sedimentary Geology*, 421, 105946.

Abebe, T., Balestrieri, M. L. and Bigazzi, G., 2010. The central Main Ethiopian rift is younger than 8 Ma: Confirmation through apatite fission-track thermochronology. *Terra Nova*, 22 (6), 470–476.

Alemseged, Z., 2023. Reappraising the palaeobiology of Australopithecus. *Nature*, 617 (7959), 45–54.

Arambourg, C. and Coppens, Y., 1967. Sur la découverte, dans le Pléistocène inférieur de la vallée de l'Omo (Éthiopie), d'une mandibule d'australopithécien. *CR Acad. Sci. Paris*, 365, 589–590.

Asefa, M., Cao, M., He, Y., Mekonnen, E., Song, X. and Yang, J., 2020. Ethiopian vegetation types, climate and topography. *Plant Diversity*, 42 (4), 302–311.

Bailey, G. N., Reynolds, S. C. and King, G. C., 2011. Landscapes of human evolution: models and methods of tectonic geomorphology and the reconstruction of hominin landscapes. *Journal of Human Evolution*, 60 (3), 257–280.

Beasley, M. M., 2016. *Seasonal precipitation at a 3.97 Ma Australopithecus anamensis site, Allia Bay, Kenya*. University of California, San Diego.

Behrensmeyer, A. K., 2006. Climate change and human evolution. *Science*, 311 (5760), 476–478.

Bobe, R., Behrensmeyer, A. K. and Chapman, R. E., 2002. Faunal change, environmental variability and late Pliocene hominin evolution. *Journal of human evolution*, 42 (4), 475–497.

Bobe, R., Manthi, F. K., Ward, C. V., Plavcan, J. M. and Carvalho, S., 2020. The ecology of Australopithecus anamensis in the early Pliocene of Kanapoi, Kenya. *Journal of Human Evolution*, 102717.

Bonini, M., Corti, G., Innocenti, F., Manetti, P., Mazzarini, F., Abebe, T. and Pecskay, Z., 2005. Evolution of the Main Ethiopian Rift in the frame of Afar and Kenya rifts propagation. *Tectonics*, 24 (1).

Bonnefille, R., 2010. Cenozoic vegetation, climate changes and hominid evolution in tropical Africa. *Global and Planetary Change*, 72 (4), 390–411.

Bosworth, W., Huchon, P. and McClay, K., 2005. *The Red Sea and Gulf of Aden basins*. Vol. 43.

Brown, F. and de Heinzelin, J., 1983. The lower Omo basin. *de Heinzelin*, 7–24.

Bryja, J., Meheretu, Y., Boratyński, Z., Zeynu, A., Denys, C., Mulualem, G., Welegerima, K., Bryjová, A., Kasso, M. and Kostin, D. S., 2022. Rodents of the Afar Triangle (Ethiopia): geographical isolation causes high level of endemism. *Biodiversity and Conservation*, 31 (2), 629–650.

Butzer, K. W. and Thurber, D., 1969. Some late Cenozoic sedimentary formations of the Lower Omo Basin. *Nature*, 222, 1138–1143.

Coppens, Y., 1978. Evolution of the hominids and of their environment during the Plio-Pleistocene in the lower Omo Valley, Ethiopia. *Geological Society, London, Special Publications*, 6 (1), 499–506.

Corti, G., Sani, F., Philippon, M., Sokoutis, D., Willingshofer, E. and Molin, P., 2013. Quaternary volcano-tectonic activity in the Soddo region, western margin of the Southern Main Ethiopian Rift. *Tectonics*, 32 (4), 861–879.

Cote, S., Kingston, J., Deino, A., Winkler, A., Kityo, R. and MacLatchy, L., 2018. Evidence for rapid faunal change in the early Miocene of East Africa based on revised biostratigraphic and radiometric dating of Bukwa, Uganda. *Journal of Human Evolution*, 116, 95–107.

Couvreur, T. L., Dauby, G., Blach-Overgaard, A., Deblauwe, V., Dessein, S., Droissart, V., Hardy, O. J., Harris, D. J., Janssens, S. B. and Ley, A. C., 2021. Tectonics, climate and the diversification of the tropical African terrestrial flora and fauna. *Biological Reviews*, 96 (1), 16–51.

Daver, G., Guy, F., Mackaye, H. T., Likius, A., Boisserie, J.-R., Moussa, A., Pallas, L., Vignaud, P. and Clarisse, N. D., 2022. Postcranial evidence of late Miocene hominin bipedalism in Chad. *Nature*, 609 (7925), 94–100.

deMenocal, P. B., 1995. Plio-pleistocene African climate. *Science*, 270 (5233), 53–59.

deMenocal, P. B., 2004. African climate change and faunal evolution during the Pliocene–Pleistocene. *Earth and Planetary Science Letters*, 220 (1–2), 3–24.

deMenocal, P. B., 2011. Anthropology. Climate and human evolution. *Science*, 331 (6017), 540–542.

DeMiguel, D. and Rook, L., 2018. Understanding climate's influence on the extinction of Oreopithecus (late Miocene, Tusco-Sardinian paleobioprovince, Italy). *Journal of Human Evolution*, 116, 14–26.

Demissew, S., Friis, I. and Weber, O., 2021. Diversity and endemism of the flora of Ethiopia and Eritrea: state of knowledge and future perspectives. *Rendiconti Lincei. Scienze Fisiche e Naturali*, 32 (4), 675–697.

Drapeau, M. S., Bobe, R., Wynn, J. G., Campisano, C. J., Dumouchel, L. and Geraads, D., 2014. The Omo Mursi formation: A window into the east African Pliocene. *Journal of human evolution*, 75, 64–79.

Dumouchel, L., 2018. *A multi-proxy analysis of Australopithecus anamensis paleoecology in the Omo-Turkana Basin.* The George Washington University.

Dumouchel, L., Bobe, R., Wynn, J. G. and Barr, W. A., 2021. The environments of Australopithecus anamensis at Allia Bay, Kenya: A multiproxy analysis of early Pliocene Bovidae. *Journal of Human Evolution*, 151, 102928.

Dumouchel, L. and Drapeau, M., 2014. Taphononic study of the fossil fauna from the Mursi Formation and Member A of the Shungura Formation, Ethiopia. *American Journal of Physical Anthropology*, March 2014.

El-Sayed, S., Murray, A. M., Kora, M. A., Abu El-Kheir, G. A., Antar, M. S., Seiffert, E. R. and Sallam, H. M., 2020. Oldest Record of African Bagridae and Evidence from Catfishes for a Marine Influence in the Late Eocene Birket Qarun Locality 2 (BQ-2), Fayum Depression, Egypt. *Journal of Vertebrate Paleontology*, 40 (3), e1780248.

Feibel, C. S. and Schwindinger, P., 2011. A Geological History of the Turkana Basin. *Evolutionary Anthropology: Issues, News, and Reviews*, 20 (6), 206–216.

Feibel, C. S. and Schwindinger, P., 2012. *Paleogeography of Lake Turkana* [online]. Available from: https://education.nationalgeographic.org/resource/paleogeography-lake-turkana/ [Accessed January 2025].

Fernandes, C. A., Rohling, E. J. and Siddall, M., 2006. Absence of post-Miocene Red Sea land bridges: biogeographic implications. *Journal of Biogeography*, 33 (6), 961–966.

Fielding, L., Najman, Y., Millar, I., Butterworth, P., Garzanti, E., Vezzoli, G., Barfod, D. and Kneller, B., 2018. The initiation and evolution of the River Nile. *Earth and Planetary Science Letters*, 489, 166–178.

Friis, I., Thulin, M., Adsersen, H. and Buerger, A.-M., 2005. Patterns of plant diversity and endemism in the Horn of Africa. *Biol. Skr*, 55, 289–314.

Frost, S. R., Ward, C. V., Manthi, F. K. and Plavcan, J. M., 2020. Cercopithecid fossils from Kanapoi, West Turkana, Kenya (2007–2015). *Journal of Human Evolution*, 102642.

Gani, N., Gani, M. and Abdelsalam, M., 2007. Blue Nile incision on the Ethiopian Plateau: Pulsed plateau growth, Pliocene uplift, and hominin evolution. *Gsa Today*, 17 (9).

Gani, N. D. and Neupane, P. C., 2018. Understanding transient landscape of the Ethiopian Plateau in relation to mantle dynamics. *Geological Journal*, 53 (1), 371–385.

García-Aguilar, J. M., Campaña, I., Martínez-Navarro, B., Guerra-Merchán, A., Rodríguez-Ruiz, M. D., Rodríguez-Gómez, G., Granados, A., León-Reina, L., Espigares, M. P. and Ros-Montoya, S., 2024. Plio-Pleistocene hydrothermal events of the Baza Basin (Betic Cordillera, SE Spain) and their paleoecological implications. *Journal of Iberian Geology*, 1–37.

Gentzis, T., Carvajal-Ortiz, H., Selim, S. S., Tahoun, S. S., El-Shafeiy, M., Ocubalidet, S. and Ali, A. A.-M., 2018. Depositional environment and characteristics of Late Eocene carbonaceous swampy tidal flat facies in the Fayoum Basin, Egypt. *International Journal of Coal Geology*, 200, 45–58.

Gheerbrant, E. and Rage, J.-C., 2006. Paleobiogeography of Africa: How distinct from Gondwana and Laurasia? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 241 (2), 224–246.

Gilbert, C., Bibi, F., Hill, A. and Beech, M., 2014. Early guenon from the late Miocene Baynunah Formation, Abu Dhabi, with implications for cercopithecoid biogeography and evolution. *Proceedings of the National Academy of Sciences*.

Gilbert, C. and Hill, A., 2022. Primates from the Baynunah Formation. 203–218.

Grossman, A., Calvo, R., López-Antoñanzas, R., Knoll, F., Hartman, G. and Rabinovich, R., 2019. First record of Sivameryx (Cetartiodactyla, Anthracotheriidae) from the lower Miocene of Israel highlights the importance of the Levantine Corridor as a dispersal route between Eurasia and Africa. *Journal of Vertebrate Paleontology* 39 (2), e1599901.

Haile-Selassie, Y., Saylor, B. Z., Deino, A., Levin, N. E., Alene, M. and Latimer, B. M., 2012. A new hominin foot from Ethiopia shows multiple Pliocene bipedal adaptations. *Nature*, 483 (7391), 565–569.

Haile-Selassie, Y. and WoldeGabriel, G., 2009. Ardipithecus kadabba: late miocene evidence from the Middle Awash, Ethiopia. Univ of California Press.

Hammond, A. S., Rook, L., Anaya, A. D., Cioppi, E., Costeur, L., Moya-Sola, S. and Almecija, S., 2020. Insights into the lower torso in late Miocene hominoid Oreopithecus bambolii. *Proc Natl Acad Sci U S A*, 117 (1), 278–284.

Harrison, T., 2010. Apes among the tangled branches of human origins. *Science*, 327 (5965), 532–534.

Holmes, R. B., Murray, A. M., Chatrath, P., Attia, Y. S. and Simons, E. L., 2010. Agamid lizard (Agamidae: Uromastycinae) from the lower Oligocene of Egypt. *Historical Biology*, 22 (1-3), 215–223.

Hunt, K. D., 1996. The postural feeding hypothesis: an ecological model for the evolution of bipedalism. *South African Journal of Science*, 92 (2), 77–90.

Jacobs, B. F., Tabor, N., Feseha, M., Pan, A., Kappelman, J., Rasmussen, T., Sanders, W., Wiemann, M., Crabaugh, J. and Massini, J. L. G., 2005. Oligocene terrestrial strata of northwestern Ethiopia: a preliminary report on paleoenvironments and paleontology. *Palaeontologia electronica [electronic resource]. Vol. 8, no. 1 (2005): 19 p.*

Johanson, D. C., 1978. A new species of the genus Australopithecus (Primates: Hominidae) from the Pliocene of eastern Africa. *Kirtlandia*, 28, 1–14.

Joordens, J. C., Feibel, C. S., Vonhof, H. B., Schulp, A. S. and Kroon, D., 2019. Relevance of the eastern African coastal forest for early hominin biogeography. *Journal of human evolution*, 131, 176–202.

Kampouridis, P., Hartung, J. and Augustin, F. J., 2023. The Eocene–Oligocene vertebrate assemblages of the Fayum Depression, Egypt. *The Phanerozoic Geology and Natural Resources of Egypt.* Springer, 373–405.

Kappelman, J., Tab Rasmussen, D., Sanders, W. J., Feseha, M., Bown, T., Copeland, P., Crabaugh, J., Fleagle, J., Glantz, M. and Gordon, A., 2003. Oligocene mammals from Ethiopia and faunal exchange between Afro-Arabia and Eurasia. *Nature*, 426 (6966), 549–552.

Keir, D., Bastow, I. D., Corti, G., Mazzarini, F. and Rooney, T. O., 2015. The origin of along-rift variations in faulting and magmatism in the Ethiopian Rift. 34 (3), 464–477.

King, G. and Bailey, G., 2006. Tectonics and human evolution. *antiquity*, 80 (308), 265–286.

Kissel, M. and Hawks, J., 2015. What are the Lothagam and Tabarin Mandibles? *PaleoAnthropology*, 2015, 37–43.

Köhler, M. and Moyà-Solà, S., 1997. Ape-like or hominid-like? The positional behavior of Oreopithecus bambolii reconsidered. *Proceedings of the National Academy of Sciences*, 94 (21), 11747–11750.

Lawrence, A. B., Hammond, A. S. and Ward, C. V., 2025. Acetabular orientation, pelvic shape, and the evolution of hominin bipedality. *Journal of Human Evolution*, 200, 103633.

Leakey, M., Grossman, A., Gutiérrez, M. and Fleagle, J. G., 2011. Faunal change in the Turkana Basin during the late Oligocene and Miocene. *Evolutionary Anthropology: Issues, News, and Reviews*, 20 (6), 238–253.

Lithgow-Bertelloni, C. and Silver, P. G., 1998. Dynamic topography, plate driving forces and the African superswell. *NATURE*, 395, 269.

Louchart, A., Wesselman, H., Blumenschine, R. J., Hlusko, L. J., Njau, J. K., Black, M. T., Asnake, M. and White, T. D., 2009. Taphonomic, avian, and small-vertebrate indicators of Ardipithecus ramidus habitat. *science*, 326 (5949), 66–66e64.

Lovejoy, C. O. and McCollum, M. A., 2010. Spinopelvic pathways to bipedality: why no hominids ever relied on a bent-hip–bent-knee gait. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365 (1556), 3289–3299.

Lovejoy, C. O., Suwa, G., Spurlock, L., Asfaw, B. and White, T. D., 2009. The pelvis and femur of Ardipithecus ramidus: the emergence of upright walking. *science*, 326 (5949), 71–71e76.

Macgregor, D., 2015. History of the development of the East African Rift System: A series of interpreted maps through time. *Journal of African Earth Sciences*, 101, 232–252.

Macgregor, D. S., 2012. The development of the Nile drainage system: integration of onshore and offshore evidence. *Petroleum Geoscience*, 18 (4), 417–431.

Manthi, F. K., Plavcan, J. M. and Ward, C. V., 2020. Introduction to special issue Kanapoi: Paleobiology of a Pliocene site in Kenya. *Journal of Human Evolution*, 102718.

Maslin, M. A., Brierley, C. M., Milner, A. M., Shultz, S., Trauth, M. H. and Wilson, K. E., 2014. East African climate pulses and early human evolution. *Quaternary Science Reviews*, 101, 1–17.

Mattingly, S., 2022. *New Eurasian Immigrants in the Late Paleogene of Africa, and the Great Old World Biotic Interchange: A Quantitative Analysis of Mammalian Dispersal.* University of Kansas.

Maxwell, S. J., Hopley, P. J., Upchurch, P. and Soligo, C., 2018. Sporadic sampling, not climatic forcing, drives observed early hominin diversity. *Proc Natl Acad Sci U S A*, 115 (19), 4891–4896.

McKee, J. K., 2017. Correlates and catalysts of hominin evolution in Africa. *Theory in Biosciences*, 136 (3-4), 123–140.

McQuarrie, N., Stock, J., Verdel, C. and Wernicke, B., 2003. Cenozoic evolution of Neotethys and implications for the causes of plate motions. *Geophysical research letters*, 30 (20).

Meredith, R. W., Janečka, J. E., Gatesy, J., Ryder, O. A., Fisher, C. A., Teeling, E. C., Goodbla, A., Eizirik, E., Simão, T. L. and Stadler, T., 2011. Impacts of the Cretaceous Terrestrial Revolution and KPg extinction on mammal diversification. *science*, 334 (6055), 521–524.

Mohr, P. and Zanettin, B., 1988. The Ethiopian Flood Basalt Province. *In:* Macdougall, J. D., ed. *Continental Flood Basalts.* Dordrecht: Springer Netherlands, 63–110.

Moucha, R. and Forte, A. M., 2011. Changes in African topography driven by mantle convection. *Nature Geoscience*, 4 (10), 707–712.

Murray, A. M., 2004. Late Eocene and early Oligocene teleost and associated ichthyofauna of the Jebel Qatrani Formation, Fayum, Egypt. *Palaeontology*, 47 (3), 711–724.

Murray, A. M., Cook, T. D., Attia, Y. S., Chatrath, P. and Simons, E. L., 2010. A freshwater ichthyofauna from the late Eocene Birket Qarun Formation, Fayum, Egypt. *Journal of Vertebrate Paleontology*, 30 (3), 665–680.

Nyblade, A. A. and Robinson, S. W., 1994. The african superswell. *Geophysical research letters*, 21 (9), 765–768.

O'Regan, H. J. and Reynolds, S., 2009. An ecological reassessment of the southern African carnivore guild: a case study from Member 4, Sterkfontein, South Africa. *Journal of Human Evolution*, 57 (3), 212–222.

Olson, S. L. and Rasmussen, D. T., 1986. Paleoenvironment of the earliest hominoids: new evidence from the Oligocene avifauna of Egypt. *Science*, 233 (4769), 1202–1204.

Orszag-Sperber, F., Plaziat, J.-C., Baltzer, F. and Purser, B., 2001. Gypsum salina–coral reef relationships during the Last Interglacial (marine isotopic stage 5e) on the Egyptian Red Sea coast: A Quaternary analogue for Neogene marginal evaporites? *Sedimentary Geology*, 140 (1-2), 61–85.

Pickford, M., Senut, B., Gommery, D. and Treil, J., 2002. Bipedalism in Orrorin tugenensis revealed by its femora. *Comptes Rendus Palevol*, 1 (4), 191–203.

Potts, R., 1998. Environmental hypotheses of hominin evolution. *American Journal Of Physical Anthropology*, 107 (S27), 93–136.

Rage, J.-C. and Gheerbrant, E., 2020. Island Africa and Vertebrate Evolution: A Review of Data and Working Hypotheses. *Biological Consequences of Plate Tectonics.* Springer International Publishing, 251–264.

Redfield, T. F., Wheeler, W. H. and Often, M., 2003. A kinematic model for the development of the Afar Depression and its paleogeographic implications. *Earth and Planetary Science Letters*, 216 (3), 383–398.

Reilinger, R. and McClusky, S., 2011. Nubia–Arabia–Eurasia plate motions and the dynamics of Mediterranean and Middle East tectonics. *Geophysical Journal International*, 186 (3), 971–979.

Retallack, G. J., 2001. Cenozoic expansion of grasslands and climatic cooling. *The Journal of Geology*, 109 (4), 407–426.

Reynolds, S. C., 2007. Mammalian body size changes and Plio-Pleistocene environmental shifts: implications for understanding hominin evolution in eastern and southern Africa. *Journal of Human Evolution*, 53 (5), 528–548.

Reynolds, S. C., Bailey, G. N. and King, G. C., 2011. Landscapes and their relation to hominin habitats: case studies from Australopithecus sites in eastern and southern Africa. *Journal of Human Evolution*, 60 (3), 281–298.

Reynolds, S. C. and Bobe, R., 2022. *African Paleoecology and Human Evolution*. Cambridge University Press.

Richmond, B. G., Begun, D. R. and Strait, D. S., 2001. Origin of human bipedalism: the knuckle-walking hypothesis revisited. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, 116 (S33), 70–105.

Rogers, N., 2006. Basaltic magmatism and the geodynamics of the East African Rift System. *Geological Society, London, Special Publications*, 259 (1), 77–93.

Rook, L., Abbazzi, L., Trebini, L., Gallai, G. and Delfino, M., 2006a. Il giacimento paleontologico di Fiume Santo. Stato delle ricerche e prospettive a dieci anni dalla scoperta. *Il giacimento paleontologico di Fiume Santo. Stato delle ricerche e prospettive a dieci anni dalla scoperta*, 1000–1009.

Rook, L., Bondioli, L., Kohler, M., Moya-Sola, S. and Macchiarelli, R., 1999. Oreopithecus was a bipedal ape after all: Evidence from the iliac cancellous architecture. *Proceedings of the National Academy of Sciences*, 96 (15), 8795–8799.

Rook, L., Gallai, G. and Torre, D., 2006b. Lands and endemic mammals in the Late Miocene of Italy: constrains for paleogeographic outlines of Tyrrhenian area. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 238 (1-4), 263–269.

Rowan, J., Du, A., Lundgren, E. J., Faith, J. T., Beaudrot, L., Campisano, C. J., Joordens, J. C., Lazagabaster, I. A., Locke, E. M. and Smail, I. E., 2024. Long-term biotic homogenization in the East African Rift System over the last 6 million years of hominin evolution. *Nature ecology & evolution*, 8 (9), 1751–1759.

Sani, F., Ghinassi, M., Papini, M., Oms, O. and Finotello, A., 2017. Evolution of the northern tip of Afar triangle: Inferences from the Quaternary succession of the Dandiero — Massawa area (Eritrea). *Tectonophysics*, 717, 339–357.

Sartori, R., 2001. Corsica—Sardinia block and the Tyrrhenian Sea. *In:* Vai, G. B. and Martini, I. P., eds. *Anatomy of an Orogen: the Apennines and Adjacent Mediterranean Basins.* Dordrecht: Springer Netherlands, 367–374.

Schettino, A., Macchiavelli, C. and Rasul, N. M. A., 2019. Plate Motions Around the Red Sea Since the Early Oligocene. *Geological Setting, Palaeoenvironment and Archaeology of the Red Sea.* 203–220.

Seiffert, E. R., 2006. Revised age estimates for the later Paleogene mammal faunas of Egypt and Oman. *Proceedings of the National Academy of Sciences*, 103 (13), 5000–5005.

Seiffert, E. R., 2012. Early primate evolution in Afro-Arabia. *Evolutionary Anthropology: Issues, News, and Reviews*, 21 (6), 239–253.

Seiffert, E. R., Simons, E. L., Clyde, W. C., Rossie, J. B., Attia, Y., Bown, T. M., Chatrath, P. and Mathison, M. E., 2005a. Basal Anthropoids from Egypt and the Antiquity of Africa's Higher Primate Radiation. *Science*, 310 (5746), 300–304.

Seiffert, E. R., Simons, E. L., Ryan, T. M. and Attia, Y., 2005b. Additional remains of Wadilemur elegans, a primitive stem galagid from the late Eocene of Egypt. *Proceedings of the National Academy of Sciences*, 102 (32), 11396–11401.

Sembroni, A., Faccenna, C., Becker, T. W., Molin, P. and Abebe, B., 2016a. Long-term, deep-mantle support of the Ethiopia-Yemen Plateau. *Tectonics*, 35 (2), 469–488.

Sembroni, A., Molin, P., Pazzaglia, F. J., Faccenna, C. and Abebe, B., 2016b. Evolution of continental-scale drainage in response to mantle dynamics and surface processes: An example from the Ethiopian Highlands. *Geomorphology*, 261, 12–29.

Sen, S., 2013. Dispersal of African mammals in Eurasia during the Cenozoic: ways and whys. *Geobios*, 46 (1-2), 159–172.

Senut, B., Pickford, M., Gommery, D. and Ségalen, L., 2018. Palaeoenvironments and the origin of hominid bipedalism. *Historical Biology*, 30 (1-2), 284–296.

Sepulchre, P., Ramstein, G., Fluteau, F., Schuster, M., Tiercelin, J.-J. and Brunet, M., 2006. Tectonic uplift and Eastern Africa aridification. *Science*, 313 (5792), 1419–1423.

Simpson, S. W., Kleinsasser, L., Quade, J., Levin, N. E., McIntosh, W. C., Dunbar, N., Semaw, S. and Rogers, M. J., 2015. Late Miocene hominin teeth from the Gona Paleoanthropological Research Project area, Afar, Ethiopia. *Journal of Human Evolution*, 81, 68–82.

Stamos, P. A. and Alemseged, Z., 2023. Hominin locomotion and evolution in the Late Miocene to Late Pliocene. *Journal of Human Evolution*, 178, 103332.

Stanhope, M. J., Waddell, V. G., Madsen, O., De Jong, W., Hedges, S. B., Cleven, G. C., Kao, D. and Springer, M. S., 1998. Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. *Proceedings of the National Academy of Sciences*, 95 (17), 9967–9972.

Steiper, M. E. and Seiffert, E. R., 2012. Evidence for a convergent slowdown in primate molecular rates and its implications for the timing of early primate evolution. *Proceedings of the National Academy of Sciences*, 109 (16), 6006–6011.

Stevens, N. J., Seiffert, E. R., O'Connor, P. M., Roberts, E. M., Schmitz, M. D., Krause, C., Gorscak, E., Ngasala, S., Hieronymus, T. L. and Temu, J., 2013. Palaeontological evidence for an Oligocene divergence between Old World monkeys and apes. *Nature*, 497 (7451), 611–614.

Stewart, K. M. and Murray, A. M., 2017. Biogeographic implications of fossil fishes from the Awash River, Ethiopia. *Journal of Vertebrate Paleontology*, 37 (1), e1269115.

Tefera, M., 2011. Wildlife in Ethiopia: endemic large mammals. *World Journal of Zoology*, 6 (2), 108–116.

Thorpe, S. K. S., McClymont, J. M. and Crompton, R. H., 2014. The arboreal origins of human bipedalism. *Antiquity*, 88 (341), 906–914.

Ukstins, I. A., Renne, P. R., Wolfenden, E., Baker, J., Ayalew, D. and Menzies, M., 2002. Matching conjugate volcanic rifted margins: 40Ar/39Ar chrono-stratigraphy of pre- and syn-rift bimodal flood volcanism in Ethiopia and Yemen. *Earth and Planetary Science Letters*, 198 (3), 289–306.

Urciuoli, A. and Alba, D. M., 2023. Systematics of Miocene apes: State of the art of a neverending controversy. *Journal of Human Evolution*, 175, 103309.

Vignaud, P., Duringer, P., Mackaye, H. T., Likius, A., Blondel, C., Boisserie, J.-R., De Bonis, L., Eisenmann, V., Etienne, M.-E. and Geraads, D., 2002. Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. *Nature*, 418 (6894), 152–155.

Villmoare, B., Kimbel, W. H., Seyoum, C., Campisano, C. J., DiMaggio, E. N., Rowan, J., Braun, D. R., Arrowsmith, J. R. and Reed, K. E., 2015. Early Homo at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. *Science*, 347 (6228), 1352–1355.

Vrba, E. S., 1993. Turnover-pulses, the Red Queen, and related topics. *American Journal of Science*, 293 (A), 418.

Vrba, E. S. and Haile-Selassie, Y., 2006. A new antelope, Zephyreduncinus oundagaisus (Reduncini, Artiodactyla, Bovidae), from the late Miocene of the Middle Awash, Afar Rift, Ethiopia. *Journal of Vertebrate Paleontology*, 26 (1), 213–218.

Wagner, P., Leaché, A., Mazuch, T. and Böhme, W., 2013. Additions to the lizard diversity of the Horn of Africa: Two new species in the Agama spinosa group. *Amphibia-Reptilia*, 34 (3), 363–387.

Wang, S. W., Boru, B. H., Njogu, A. W., Ochola, A. C., Hu, G. W., Zhou, Y. D. and Wang, Q. F., 2020. Floristic composition and endemism pattern of vascular plants in Ethiopia and Eritrea. *Journal of Systematics and Evolution*, 58 (1), 33–42.

White, T. D., Ambrose, S. H., Suwa, G., Su, D. F., DeGusta, D., Bernor, R. L., Boisserie, J.-R., Brunet, M., Delson, E. and Frost, S., 2009. Macrovertebrate paleontology and the Pliocene habitat of Ardipithecus ramidus. *science*, 326 (5949), 67–93.

White, T. D., Suwa, G. and Asfaw, B., 1994. Australopithecus ramidus, a new species of early hominid from Aramis, Ethiopia. *Nature*, 371 (6495), 306–312.

White, T. D., Suwa, G. and Asfaw, B., 1995. Corrigendum: Australopithecus ramidus, a new species of early hominid from Aramis, Ethiopia. *Nature*, 375 (6526), 88.

Winder, I. C., Deves, M. H., King, G. C. P., Bailey, G. N., Inglis, R. H. and Meredith-Williams, M., 2015. Evolution and dispersal of the genus Homo: A landscape approach. *J Hum Evol*, 87, 48–65.

Winder, I. C., King, G. C., Devès, M. and Bailey, G. N., 2013. Complex topography and human evolution: the missing link. *Antiquity*, 87 (336), 333–349.

Xue, L., Alemu, T., Gani, N. and Abdelsalam, M., 2018. Spatial and temporal variation of tectonic uplift in the southeastern Ethiopian Plateau from morphotectonic analysis. *Geomorphology*, 309, 98–111.

Yalden, D. and Largen, M., 1992. The endemic mammals of Ethiopia. *Mammal Review*, 22 (3-4), 115–150.

Zwaan, F., Corti, G., Keir, D. and Sani, F., 2019. A review of tectonic models for the rifted margin of Afar: implications for continental break-up and passive margin formation. *Journal of African Earth Sciences*, 103649.

Zwaan, F., Corti, G., Sani, F., Keir, D., Muluneh, A., Illsley-Kemp, F. and Papini, M., 2020. Structural analysis of the Western Afar Margin, East Africa: evidence for multiphase rotational rifting. *Tectonics*, 39 (7), e2019TC006043.