The co-evolution of Africa's eastern margin and its primate fauna:

implications for hominin evolution

by

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A dissertation submitted to Nelson Mandela University in fulfilment of the requirement for the degree of Master of Science in Geosciences

December 2022

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DECLARATION:

In accordance with Rule G4.6.3, I hereby declare that the above mentioned dissertation is my own work and that it has not previously been submitted for assessment to another University or for another qualification.

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ABSTRACT

I investigated potential links between the diversification of African primate lineages and the physical evolution of the continent. I compared published phylogenetic trees based on mitochondrial and nuclear DNA for five clades: (a) Lorisoidea (galagos and pottos); (b) arboreal guenon monkeys (*Cercopithecus* and its allies); (c) living apes (including humans); (d) Papionini (baboons); and (e) savanna or “vervet” monkeys (*Chlorocebus*). I compared primate divergence dates with the ages of tectonic events, patterns of climatic change, and their palaeo-vegetational consequences. Based on present primate distributions, I estimated likely geographic locations of the divergence events. Finally, I compared the phylogenetic patterns of the primate clades with hominin evolutionary scenarios.

Phylogenetic comparisons indicated three time periods when rates of speciation increased across the five primate clades: the Eocene – Oligocene transition (34 – 32 Ma); the mid-late Miocene (10 – 5 Ma); and the Pliocene – Pleistocene transition (2.7 – 2.3 Ma). Concentrated bursts of lineage splitting indicate a broadscale causal relationship between environmental change and lineage divergence. Human evolution followed similar biogeographic patterns to those of other primate clades. Tectonic events, climatic changes and palaeo-vegetational shifts are intimately connected, and have synergistic effects on biotic diversity. Tectonic events influence climatic change through their effects on oceanic circulation, planetary temperatures and rainfall patterns. Additionally, tectonic uplift and erosion may create geographic barriers to organismal dispersal across the continent, increasing the likelihood of geographic separation of populations and speciation.

Recently evolved primate species show high levels of hybridisation for several generations after their initial divergence. Genus *Homo* generated ~10 species over 2.5 Ma. The emergence of these taxa likely involved substantial hybridisation, as demonstrated by the presence of Neanderthal genes within the *H. sapiens* genome. I suggest that this hybridisation contributed to the difficulties palaeoanthropologists often experience in distinguishing fossil hominin taxa.

Key words: apes, cercopithecins, hominins, lorisoids, palaeoclimates, papionins, phylogenies, primates, tectonics

ACKNOWLEDGEMENTS

I would like to acknowledge my family first and foremost for being supportive of me throughout this project, and secondly my supervisors for believing that I could finish even when I did not believe it myself. I would like to thank the late Prof Maarten de Wit for all the advice he gave me with regard to this project. I am glad to know he felt it was a good dissertation before his passing. I would like to thank Dr Bastien Linol for not hesitating to take over my project after the passing of Prof de Wit, I appreciate you reading it and offering help where needed. I would like to thank Prof Judith Masters who has spent endless hours on my project making sure it was my best work and that it will open doors for me, not just help me to graduate. And finally, I would like to thank the NRF and AEON for funding this project.

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CHAPTER ONE: INTRODUCTION

Early human evolution took place across the African continent within a diverse array of contexts, including rain forests, woodlands and bushveld that offered varying food sources, and different risks and predators. These changing environments demanded behavioural and physiological adaptations to cope with changing needs for survival. Humans evolved within a much wider phylogenetic context than is often considered: the tribe Hominini is one branch of a bushy evolutionary tree that also comprises other apes, monkeys and baboons, and nocturnal tooth-combed primates, with which our ancestors shared their habitats. The complex hominin lineage emerged against a changing topography driven by tectonic developments of the East African Rift System (EARS), and changes in climate and vegetation during the Cenozoic.

For this study, I compiled the following datasets: (1) phylogenetic data for five African primate clades (lorisoids, hominoids, arboreal cercopithecins (or guenons), semi-terrestrial guenons, and papionins); (2) a summary of major tectonic events since 60 million years ago (Ma), and (3) a summary of Africa's palaeoclimatic history. I compared lineage divergence times of the three primate clades chiefly adapted to tropical and subtropical forest habitats (lorisoids, arboreal guenons and apes) with those of the two clades adapted to more open habitats, including grassland and woodland (semi-terrestrial guenons, baboons) in order to assess potential causal links between palaeo-environmental changes and primate diversification.

Finally, I summarised major aspects of hominin evolution in Africa based on the published fossil record and hypotheses of relationship between taxa expressed in the palaeo-anthropological literature, and compared this information with the patterns shown by the non-human primate clades. My aim was to explore how environmental changes are reflected in primate clades occupying different habitats at different time scales, and to track how such changes echo the varying evolutionary scenarios that have been proposed for the emergence of hominin genera since ~8 Ma.

1.1 The co-evolution of Earth and life

The evolution of Earth's physical geography is intimately related to the evolution of the life forms that inhabit its surface. Throughout the fossil and geological records there is evidence that major tectonic and climatic changes coincide with the extinction and emergence of faunal and floral lineages (Couvreur et al. 2021) (Figure 1.1). The oldest meteorites that have been dated scientifically place the age of Earth between 4 500 and 4 600 Ma (Hazen 2010), while the earliest evidence of life from the fossil record dates to at least 3 770 Ma, and possibly even 4 280 Ma (Dodd et al. 2017). Most scientists work on the assumption that life originated in Earth's oceans, although others have proposed that meteorites containing traces of amino acids have landed on Earth, and that even microbes could have been imported to Earth by extraterrestrial bodies (e.g., Wickramasinghe et al. 2003), positing that life on Earth may have an extraterrestrial source.

Eukaryotic (or complex) cells, which made multicellularity possible, appear to have arisen as a result of endosymbiosis (Sagan 1967), or the engulfing of organelles to form cellular “communities” with diverse functions. Knoll et al. (2006) suggested that this event occurred between 1 300 and 720 Ma, but the Cambrian “explosion” or radiation, during which all known animal phyla emerged (Gould 1989), only occurred much later, at 541 Ma (Figure 1.1).

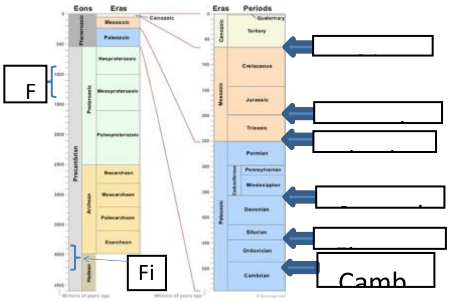


Figure 1.1. Simplified geological record of Earth history (adapted from https://stratigraphy.org/chart). Arrows indicate the first potential evidence of life, the first formation of eukaryotes (nucleate cells), the first evidence of both living and extinct phyla, and the five major mass extinctions experienced during the Phanerozoic. Numbers are in millions of years (Ma).

The geological record indicates that life on Earth has experienced five major mass extinction events within the last 450 Ma, each of which has been linked to factors affecting either Earth’s climate or tectonics. In all five cases, the extinction of the faunas and floras was followed by the relatively rapid evolution and radiation of new life forms better adapted to the new environments, eventually leading to today’s ecosystems. For example, jawless fishes (Agnatha) were largely replaced by jawed fishes 443.8 Ma, yet some agnathans (lampreys and hagfish) still survive today.

The first mass extinction event is known as the Ordovician-Silurian extinction (445 Ma), and was followed by the emergence of mosses and liverworts, flightless insects, spiders, scorpions and cartilaginous jawed fishes. The second mass extinction event occurred in the late Devonian (359 Ma), and was succeeded by the emergence of ferns, amphibians and flying insects. After the third extinction event at the Permian-Triassic boundary (252 Ma), land vertebrates began to diversify. Terrestrially, this turnover is best preserved in the Karoo stratigraphy of South Africa. The new vertebrate faunas included dinosaurs, crocodylians and mammals, while the floras included the first conifers (Anderson and Anderson 1983). The fourth mass extinction, which marks the Triassic-Jurassic boundary (201 Ma), was followed by the emergence of flowering plants, which co-evolved with insect pollinators, whilst dinosaurs and crocodylians diversified. The fifth major extinction event was the Cretaceous-Palaeocene extinction (66 Ma), in which 75% of plants and animals became extinct. The interordinal diversification of placental mammals has been linked to this event (Wible et al. 2007), although other authors place it much earlier (Murphy et al. 2001). Bininda-Emonds et al. (2007) published a supertree that shows that the diversification rate of mammals remained constant throughout the Mesozoic-Cenozoic transition, and that major mammalian evolutionary events likely occurred earlier. Around 93 Ma and 85 Ma there were significant decreases in diversification rates after the emergence and initial radiation of the placental superorders. The mass extinction at 66 Ma may have been triggered by a bolide striking Earth's surface, sending up clouds of dust that blocked out the sun and prevented photosynthesis (Alvarez et al. 1980). Alternatively, a similar scenario may have resulted from rapid volcanic explosions preserved across the Large Igneous Provinces (LIP) in India (Bond and Wignall 2014).

Mass extinction events represent critical changes in the evolution of biodiversity; they are extreme but rare events. Most studies in evolutionary biology focus on more localised environmental changes, where alterations in climate and vegetation drive the extinction and origin of species. These gradual changes in local habitats relate to steady levels of speciation and extinction.

1.2 Environmental change and natural selection

Charles Darwin's model of natural selection formulated in the mid-1800s is founded on three pre-conditions: (1) over-fecundity, or the tendency of organisms to produce more offspring than the environment can sustain; (2) variation in the ability to survive and reproduce; and (3) heritability of some of these traits enhancing survival and reproduction (Lewontin 1974). The result of these three processes is that some individuals survive better than others, and leave more offspring in succeeding generations; hence the species' gene pool includes a disproportionate frequency of their genes. Darwin's major work, first presented in 1858 along with its co-discoverer

Alfred Wallace, proposed that natural selection drove both extinction and the emergence of new species (Darwin and Wallace 1858).

Natural selection is considered the driver of environmental adaptation, particularly in the face of changing climate, as well as competition among individuals. Of these two forces, competition is the weaker, as it tends to be inconsistent (Wiens 1977). Populations of species that cover a wide geographical range are more likely to experience different competitors. No phenotype is identical under all environmental conditions (Lewontin 1974), meaning that when the habitat changes, different phenotypes are competitively superior. The major driver of natural selection is thus environmental change, and hence tectonic and climatic events will generate new pressures of natural selection, resulting in either change within lineages, or extinction.

The effectiveness of natural selection is directly proportional to the amount of heritable variation in a population (Lewontin 1974), which implies that the larger the population, the higher the level of variation, and hence that selection or extinctions should be most effective in large populations. While this is certainly true for stabilising or negative selection – which tends to suppress extreme phenotypes – the rapid fixation of new variants will be much more likely and more rapid in small populations, as indeed will be the loss of new variants, as stochastic forces have more drastic effects (Wright 1982).

Speciation – or the emergence of a new genomic system – is most likely to occur in small populations under strong pressures of natural selection (Wright 1931). These conditions pertain when dramatic changes disrupt previously continuous biomes, like forests or grasslands, or create physical barriers that separate biomes (e.g., rivers or mountains). The isolation of small populations under new selective pressures can therefore drive the emergence of new gene combinations, some of which will be sufficiently suited to the new conditions to allow their survival. These lineages may then emerge as new species.

1.3 Sources of information regarding evolutionary scenarios

The reconstruction of evolutionary history is based on a combination of short-term observable processes (described above) and their extrapolation over time, as well as both direct and indirect data sources. The fossil record provides direct evidence of organisms that have existed during Earth’s history, but need to be reconstructed and interpreted by palaeontologists with specialist knowledge of the groups in question and robust dating information. Moreover, it is likely that fossils only represent a very small percentage of species that ever existed. Since the 1980s, reconstructions of the evolutionary histories of living organisms using comparative molecular analyses have come to dominate the research conducted biologists interested in evolutionary processes. I discuss these data sources below.

1.3.1 The fossil record

The fossil record is comprised of organisms that were preserved in sediments through most of geological time, some of which have living representatives while others do not. The record is incomplete and favours animals with hard, mineralised shells, teeth, skeletons or cuticles, and particularly those that lived in the ocean or lacustrine environments. Only a fraction of the organisms that occurred on Earth has been preserved, and often stratigraphic records represent more erosion than preservation (Ager 1993). Because fossilisation and rediscovery are probabilistic processes, we are unlikely to find information regarding a taxon's existence in the fossil record until the organisms were present in detectable numbers (Tavaré et al. 2002).

Information from the fossil record can be used to infer when organisms lived relative to each other in geological time, and how they were related to each other based on anatomical similarities in preserved body parts. Fossils can also be used to calibrate lineage divergence dates using molecular clock analyses (section 1.3.2). If a fossil contains sufficient morphology to be allied with a living group, it will provide a minimum age estimate of when that lineage emerged.

1.3.2 Molecular phylogenetic analysis

Since the 1960s, evolutionary geneticists have been working towards a means of identifying evolutionary relationships using molecular information rather than anatomical or morphological similarity. This is because morphological similarity may be influenced by growth processes and the environment in which an organism develops (Lewontin 1974). Through natural selection, organisms may come to look more similar than would be expected from their real relationship for adaptive reasons, or may look more distinct and distantly-related than they really are. In the previous century, biologists began by studying chromosome complements (karyotypes) and allozymes – i.e., variant forms of enzymes comprised of slightly different amino acid sequences – to gain a different insight into species relationships. Today, most researchers compare amino acid, DNA or RNA nucleotide sequences directly. The discovery of the Polymerase Chain Reaction by Kary Mullis in 1983 changed molecular genetics dramatically, and led to the compilation of databases that allowed sequence comparisons among large numbers of species.

Assessing evolutionary relatedness on the basis of nucleotide sequences, however, is far from straight-forward (Felsenstein 1988). Only four bases contribute to the DNA molecule: adenine (A), cytosine (C), guanine (G) and thymine (T). Changes in nucleotide sequences occur when one or several nucletotides are deleted or inserted, or when one nucleotide is replaced by another (i.e., substitution). Assuming all replacements are equally likely, a base will be substituted by an identical base 25% of the time. In practice, the bases come in two forms: purines (A and G) and pyrimidines (C and T), which differ in their molecular size. A purine is more likely to be replaced by a purine, and a pyrimidine likewise by a pyrimidine. Such replacements are called transitions, and occur more readily because of molecular dynamics than transversions, or the replacement of a purine by a pyrimidine, or *vice versa*. Furthermore, the fact that bases pair up in the interior of the DNA double helix means that C and G must be partners, as must A and T. This means that identifying the number of base substitutions that have occurred within a given stretch of DNA over time can be complicated by saturation, i.e., repeated substitutions at a single site, often by the same kind of molecule. Analytical methods in molecular genetics are aimed at estimating the actual number of substitutions likely to have taken place, given the constraints of nucleic acid structures and the base composition of the sequence (Felsenstein 1988; Masters 2007).

1.4 Dating the past

1.4.1 Geological dating methods

There are different ways of assigning the age of a sedimentary rock layer, and the fossil remains found in them. An absolute age can be calculated through the use of radiometric dating of minerals, or a relative age can be determined using data related to palaeomagnetism, stable isotope ratios and biostratigraphy, all of which can place a fossil within a defined time interval.

An absolute age is assigned to a mineral radiometrically by measuring the amount of decay of a radioactive isotope with a known half-life. Different radioactive isotopes can be used. Slower decaying isotopes (uranium-lead, uranium-thorium, and potassium-argon isotopes) are used for measuring longer periods of time. Radiocarbon dating is generally applied to organic materials that are less than 50 ka.

Fission track dating involves the assessment of tracks left by fission events in some uranium-bearing minerals. The number of fission tracks produced by electrons during the spontaneous decay of Uranium-238 in common accessory minerals provides an estimate of the time at which the rock cooled below closure temperature. Fission track dating is used in research aimed at calculating the erosion rates of mountain belts, finding the source or provenance of sediments, studying the thermal evolution of basins, and dating and provenance determination of archaeological artefacts. Surface exposure dating is used to calculate the amount of time that a rock has been exposed at or near the surface of the earth.

1.4.2 Molecular dating methods

Molecular dating is based on estimating the number of molecular substitutions that has occurred over a given period of time among lineages, and extrapolating, according to a given mutation rate, how long ago those lineages are likely to have been separated. Confidence intervals may be considerable, covering millions of years, depending on the selective and structural constraints operating on the molecules. In order to arrive at an appropriate measure of elapsed time, the mutation rate may be calibrated according to a key fossil, which contains an indication of the minimum time by which a divergence must have occurred (Forest 2009).

The molecular clock hypothesis was originally proposed by Zuckerkandl and Pauling (1965), who inferred that the degree of difference between the amino acid sequences in the proteins of any two species should be proportional to the time elapsed since divergence from their last common ancestor. In the 1970s, the studies became more and more focussed on DNA rather than proteins, but the fact that DNA is composed of only 4 bases (see 1.3.2 above) made it difficult to estimate the number of duplicated substitutions. Over the past few decades, our understanding of molecular evolutionary dynamics has undergone a revolution, and methods of estimating rates of sequence change have become very sophisticated (Huelsenbeck et al. 2000; Yang 2004; Drummond et al. 2005; Rutschmann 2006; Wagner 2019). There are two methods for calibrating the molecular clock using fossil data: node calibration and tip calibration, both of which generally result in age uncertainity of less 1 Ma.

Node calibration

Node calibration fixes the divergence between two lineages on the age of a common ancestral fossil, which then defines the minimum age of the two lineages. Because of the relative unlikelihood of fossilisation in any given instance, compounded with the unlikelihood of fossil discovery, the actual common ancestor of a clade can never be known. To account for this problem, in node calibration analysis a maximum clade age must be assessed. There are different ways to determine the maximum clade age using birth-death (i.e., speciation-extinction) models viz. fossil stratigraphic distribution analyses or taphonomic controls. Instead of using birth-death models, the prior probability of the divergence time can be established and used to calibrate the clock. Several prior probability distributions exist, the most common of which are normal, lognormal, exponential, gamma and uniform. These distributions are used to express the probability of the true age of divergence in contrast to the age of the fossil (Wagner 2019).

Tip calibration

This is a method of calibration in which fossil taxa are placed at the tip of the tree and treated as taxa. This requires generating a matrix that includes a molecular dataset for extant taxa as well as a morphological dataset for both extinct and extant data. The difference between node calibration and tip calibration is that the reconstructed tree topology places the fossils within the time frame of their existence on Earth. Combined molecular and and morphological models allow morphological character states to place the fossils. This method of calibration includes all relevant fossil taxa during calibration, and not only the oldest fossil of each clade (Forest 2009; Wagner 2019).

1.5 Aims and objectives of the study

My aim was to compare patterns of evolutionary radiation in five clades of African primates that took place over various time frames between the Eocene and the Holocene (from 56 Ma to 10 ka ago), in order to explore potential links between major events in primate (including human) evolution in Africa and its regional tectonic and climatic evolution. I first characterised the pattern and timing of recently published phylogenetic trees for the following clades: (a) Lorisoidea (galagos and pottos); (b) the living African apes (including humans); (c) arboreal guenon monkeys (Genus *Cercopithecus* and its allies); (d) Papionini (baboons); and (e) savanna or “vervet” monkeys (Genus *Chlorocebus*). Where possible, I compared the results obtained from mitochondrial DNA (mtDNA) sequences with those based on nuclear DNA (nDNA). The mutation rate of mtDNA is more rapid than that of nDNA, which can lead to artificial divergence age estimates. Additionally, the fact that mtDNA is maternally inherited, rather than passed on by both parents, means mtDNA tree topologies are particularly susceptible to hybridisation events. Hybridisation between distinct species is rare, but has been observed at relatively high frequencies between some primate species, e.g., within the genus *Cercopithecus* (Detwiler et al. 2005). A close relationship between lineages revealed by mtDNA may hence be the result of hybridisation rather than evidence of common ancestory.

I then compared the age estimates of major evolutionary divergences within the five clades of living African primates with dates of geotectonic events that infuenced the landscapes, as well as with patterns of climatic change, and the consequences such changes might have had for patterns and types of vegetation. Based on the current distributions of the descendant species in each of these clades, I then proposed the most likely geographic localities of the major divergence events. Finally, I compared the evolutionary patterns evinced by the molecular phylogenies of the non-human primate clades with hominin evolutionary scenarios. Unlike most non-human African primates, the tribe Hominini is represented by a sole surviving species. Hominin fossils are fragmentary and sparsely distributed. My final aim was, therefore, to investigate whether a comparison of divergence times estimated from hominin phylogeny with those calculated for other primate lineages evolving alongside our ancestors could provide insights into the drivers of human evolution.

CHAPTER TWO: AFRICAN PRIMATE EVOLUTION AND DIVERSITY

2.1 Primate origins and early evolution

Molecular phylogenetic studies place the origin of crown primates (i.e., extant primate lineages) in the latest Cretaceous around 70 Ma. Perelman et al. (2011), using a dataset of almost 35,000 base pairs (bp), estimated this time of origin to occur between 90 and 80 Ma. More recent studies have proposed that the origin is likely to be younger (Springer et al. 2012: 71 – 63 Ma; Reis et al. 2018: 79 – 70 Ma). This period was an extremely warm period in Earth's history. Jenkyns et al. (2004) estimated from a sedimentary core using TEX_{86}, which they described as a "palaeothermometer" based on the composition of membrane lipids in marine plankton, that 70 Ma the sea surface temperatures of the Arctic Ocean were 15°C on average, slightly cooler than the 20°C estimated for the middle Cretaceous (90 Ma). Hence, no matter which date proves more accurate, primates emerged during a very warm climatic regime, or 'hothouse'.

The world's oldest primate fossils are found in Africa. *Altiatlasius koulchii* consists of ten isolated teeth found in a Late Palaeocene quartzitic sequence (Sigé et al. 1990) in the High Atlas Mountains of Morocco, and is approximately 57 Ma. The fossil has been classified as an early omomyiform, a basal primate, or a stem simian related to crown monkeys and apes. Although there is no consensus on what kind of primate it is, most researchers agree that *Altiatlasius* was related to modern primates (Fleagle 2013). The fact that fossils can only give a minimal age of appearance means that this fossil hypodigm is unlikely to be evidence of the first emergence of primates.

Using a large concatenated molecular dataset (69 nDNA gene segments, 10 mtDNA gene sequences) and an ancestral area reconstruction, Springer et al. (2012) concluded that primates are most likely to have originated in Asia. Beard (1998) also identified Asia as the most likely place of primate origins, because their closest living and extinct relatives have been found there. Among living mammals, primates are most closely related to Scandentia (tree shrews) and Dermoptera (colugos or flying "lemurs"). Their extinct sister-clade is likely to be the Plesiadapiformes (Silcox et al. 2008), fossils of which have been found in sediments dated from 65 to 37 Ma across the northern hemisphere continents. Plesiadapiforms have never been found in Africa. Therefore, consensus among primate evolutionists is that primates originated in Asia, and emigrated to the African continent between 70 and 60 Ma.

Most primatologists also agree that the order Primates falls naturally into two suborders: (1) Haplorhini (Pocock 1918), embracing the tarsiiforms, monkeys and apes; and (2) Strepsirrhini (Geoffroy Saint-Hilaire 1812), including the lemurs, galagos, lorises and pottos. When the first fossil Euprimates (i.e., primates of modern aspect) appeared in North America and Eurasia in the Early Eocene, ~55 Ma, both suborders were apparently present (Fleagle 2013). Fossils attributed to the family Omomyidae are allied with the haplorhines, while specimens identified as members of the infraorder Adapiformes are linked consistently with the strepsirrhine primates (Fleagle 2013) (Table 2.1).

Table 2.1. Higher level primate taxonomy (Groves 2001; Masters et al. 2013)

- Order Primates
  - Suborder Strepsirrhini
    - Infraorder Adapiformes†
      - Family Adapidae†
      - Family Notharctidae†
      - Family Sivaladapidae†
    - Infraorder Chiromyiformes
      - Family Daubentoniidae (aye-ayes)
    - Infraorder Lemuriformes (other Malagasy strepsirrhines)
      - Family Cheirogaleidae (dwarf lemurs and lepilemurs)
      - Family Indriidae (indris, sifakas and woolly lemurs)
      - Family Lemuridae (true lemurs and bamboo lemurs)
    - Infraorder Lorisiformes (Afro-Asian strepsirrhines)
      - Family Galagidae (busbabies)
      - Family Lorisidae (lorises and pottos)

  - Suborder Haplorhini
    - Infraorder Omomyiformes†
      - Family Omomyidae†
    - Infraorder Tarsiiformes (tarsiers)
      - Family Afrotarsiidae†
      - Family Tarsiidae
    - Infraorder Simiiformes (monkeys and apes)
      - Parvorder Platyrrhini (New World monkeys)
        - Family Aotidae (night monkeys)
        - Family Atelidae (spider, woolly and howler monkeys)
        - Family Cebidae (capuchins and squirrel monkeys)
        - Family Pitheciidae (sakis, titis and uakaris)
      - Parvorder Catarrhini (Old World monkeys and apes)
        - Family Oreopithecidae†
        - Family Parapithecidae†
        - Family Pliopithecidae†
        - Family Proconsulidae†
        - Family Victoriapithecidae†
        - Family Cercopithecidae (Old World monkeys)
        - Family Hylobatidae (lesser apes)
        - Family Hominidae (great apes)

† Extinct

2.2 Africa’s primate fauna and its evolution

Living primates are largely distributed across the tropical (Couvreur et al. 2021) and subtropical regions of the world, usually in forest or woodland areas (Fleagle 2013). Living strepsirrhines are found in such habitats in Africa, Madagascar and South-east Asia. Living haplorhines occur in Africa, South-east Asia, Japan, and Central and South America. Only Africa and South-east Asia host a primate fauna that includes both haplorhine and strepsirrhine faunas.

Strepsirrhines embrace the “tooth-combed primates”: the Lemuriformes (lemurs) and Chiromyiformes (aye-ayes) of Madgascar, and the Lorisiformes of Africa and South-east Asia (Groves 2001; Masters et al. 2013). The lorisiform primates comprise two families that have very different lifestyles: the slow-climbing lorisids (Lorisidae), which include the pottos of Africa and the lorises of Asia, and the active, leaping bushbabies (Galagidae), which are restricted to sub-Saharan Africa. Strepsirrhines and haplorhines seem to have diverged shortly after the appearance of Euprimates, with molecular dates ranging from 87 Ma (Perelman et al. 2011) to 67 Ma (Springer et al. 2012). Strepsirrhini then split into four lineages between 69 Ma (Perelman et al. 2011) and 55 Ma (Springer et al. 2012) (Table 2.1): (1) the Adapiformes (now extinct); (2) the Chiromyiformes (aye-ayes) and (3) Lemuriformes of Madagascar; and (4) the Lorisiformes of Africa and Asia. The African lorisiforms then diverged into the bushbaby and potto clades between 44 Ma (Pozzi 2016) and 32 Ma (Springer et al. 2012).

Suborder Haplorhini is made up of one extinct and two living infraorders (Table 2.1): (1) the Omomyiformes (now extinct), (2) the Tarsiiformes (tarsiers), presently confined to the islands of South-east Asia; and (3) the Simiiformes (Hoffstetter 1974), or monkeys and apes. Apes only occur in the Old World, i.e., Africa and Eurasia, along with the Old World monkeys, and together they make up the parvorder Catarrhini. The New World monkeys of South and Central America constitute the parvorder Platyrrhini. Apes are classified within the superfamily Hominoidea, which comprises two living families: (1) the lesser apes, or gibbons, Family Hylobatide; and (2) the great apes including Asian orang-utans and African great apes: chimpanzees, gorillas and humans, Family Hominidae. Old World monkeys constitute the superfamily Cercopithecoidea, which consists of a single living family, Cercopithecidae (Table 2.1).

It is often assumed that monkeys must have evolved before hominoids, but this anthropocentric view is erroneous. Hominoids and cercopithecoids diverged from a common ancestor during the Oligocene some 30 Ma. This date is significant both for tectonic and palaeoclimatic reasons, discussed in sections 3.2 and 4.2.2, below. Fossil evidence places the minimum age of the split at 23 Ma (Walker and Shipman 2005; Stevens et al. 2013), while molecular clock dating gives a slightly older range of dates: 36.4-26.9 Ma (Steiper and Young 2006); 31.6 Ma (Perelman et al. 2011); 26.5-21.9 Ma (Roos et al. 2011). The majority of African primate fossils from the Miocene period have been classified as apes, suggesting either that monkeys were rare during this epoch and only diversified later, or that they occupied parts of the continent where fossils have yet to be found, or are areas of poor preservation.

The Cercopithecidae (Table 2.2) diverged into two subfamilies in the mid-Miocene (18-16 Ma; Perelman et al. 2011; Springer et al. 2012): (1) the Cercopithecinae or cheek-pouched monkeys, including baboons, guenons and macaques, and (2) the leaf-eating Colobinae. Colobines have sacculate stomachs that allow them to retain plant matter for long periods to enable the digestion of cellulose. They also lack a thumb, which is the root of their name, taken from the Greek kolobos, meaning mutilated. The African colobine radiation is modest, including only three genera. Most of their radiation took place in Asia, approximately 11 Ma ago.

The subfamily Cercopithecinae consists of two tribes (Table 2.2): (1) the Cercopithecini or guenon monkeys (arboreal and semi-terrestrial); and (2) the Papionini, i.e., savanna baboons, drill-mangabeys, mandrills, baboon mangabeys, the kipunji mangabey and gelada baboons. All of South Africa’s indigenous non-human primates fall within this subfamily. Like the subfamily Colobinea, most of the macaques evolved in Asia: only one species, the Barbary macaque (*Macaca sylvanus*), is found in Africa (Morocco and Algeria). The cercopithecins are a relatively recent and diverse radiation, comprising 6 genera and at least 34 species (Lo Bianco et al. 2017) including Allen’s swamp monkey, the talapoins, the patas and savanna monkeys (vervets), and the arboreal guenons.

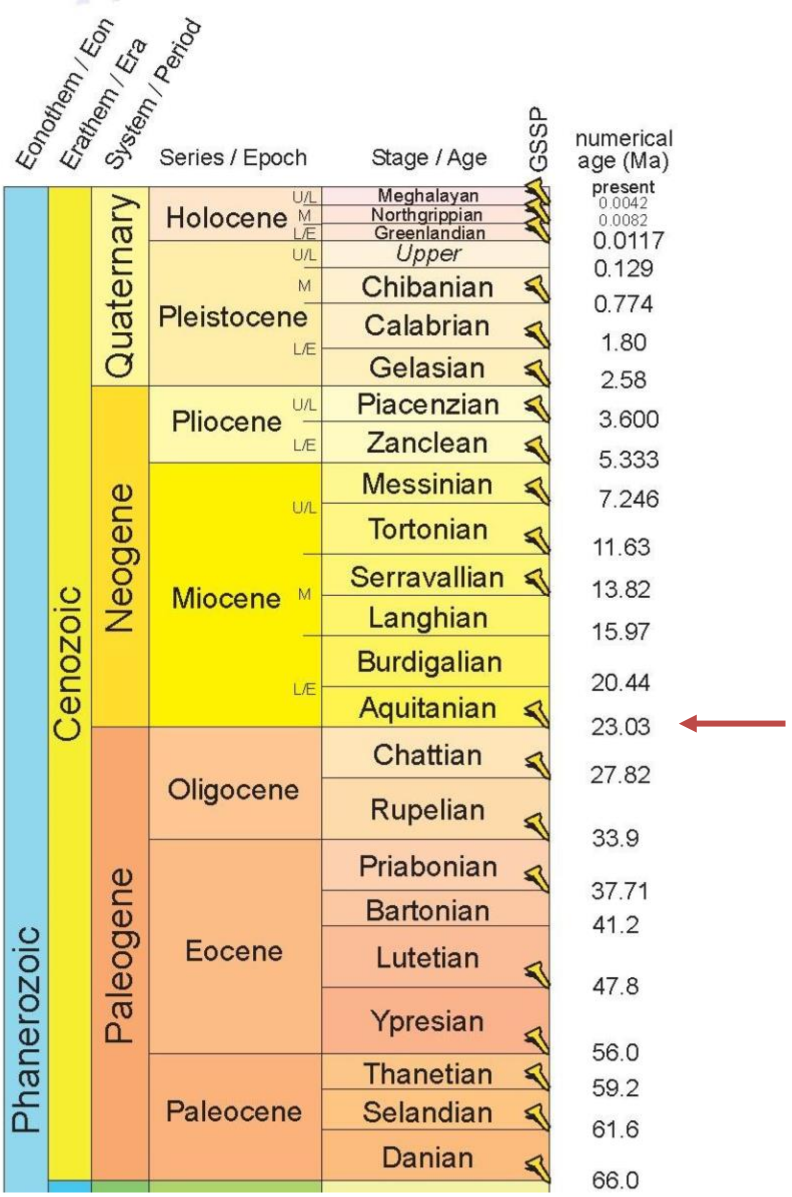
Papionins and cercopithecins diverged between 15 and 11 Ma (Lo Bianco et al. 2017). While both tribes have arboreal and terrestrial members, the papionins are mostly terrestrial, while the cercopithecins are mainly arboreal.

Table 2.2. Taxonomy of Superfamily Cercopithecoidea (Groves 2001)

- Superfamily Cercopithecoidea
    - Family Cercopithecidae
        - Subfamily Cercopithecinae (cheek-pouched monkeys)
            - Tribe Cercopithecini (guenons and allies)
                - Genera *Allenopithecus, Allochrocebus, Cercopithecus, Chlorocebus, Erythrocebus, Miopithecus*
            - Tribe Papionini (baboons, macaques and mangabeys)
                - Genera *Cercocebus, Lophocebus, Macaca, Mandrillus, Papio, Theropithecus*
        - Subfamily Colobinae (leaf-eating monkeys)
            - Genera *Colobus, Nasalis, Piliocolobus, Presbytis, Procolobus, Pygathrix, Rhinopithecus, Semnopithecus, Simias, Trachypithecus*

2.3 Africa’s non-human primate fossil record

Africa’s primate fossil record covers most of the Cenozoic era (Table 2.3). Despite being the provenance of the oldest ‘undoubted’ fossil primate, however, Africa’s fossil record of non-human primates is limited and patchy, with the exception of the diverse record of Miocene apes. This may be due to the often condensed and sporadic Cenozoic sedimentary sequences preserved on the continent.



Eonothem / Eon	Erathem / Era	System / Period	Series / Epoch		Stage / Age	GSSP	numerical age (Ma)
							present
Phanerozoic	Cenozoic	Quaternary	Holocene	U/L	Meghalayan	✓	0.0042
				M	Northgrippian	✓	0.0082
				L/E	Greenlandian	✓	0.0117
			Pleistocene	U/L	Upper		0.129
				M	Chibanian	✓	0.774
				L/E	Calabrian	✓	1.80
					Gelasian	✓	2.58
		Neogene	Pliocene	U/L	Piacenzian	✓	3.600
				L/E	Zanclean	✓	5.333
			Miocene	U/L	Messinian	✓	7.246
					Tortonian	✓	11.63
				M	Serravallian	✓	13.82
					Langhian		15.97
				L/E	Burdigalian		20.44
					Aquitanian	✓	23.03
		Paleogene	Oligocene		Chattian	✓	27.82
					Rupelian	✓	33.9
			Eocene		Priabonian	✓	37.71
					Bartonian		41.2
					Lutetian	✓	47.8
					Ypresian	✓	56.0
			Paleocene		Thanetian	✓	59.2
					Selandian	✓	61.6
					Danian	✓	66.0

Table 2.3. Major divisions of the Cenozoic era (https://stratigraphy.org/chart). The first homonoids occur at the Oligocene-Miocene transition around 25-20 Ma, during the onset of moonsoons and upwelling in the Arabian Sea (red arrow).

Ancestral primates were very different from their extant descendants, and some ancient fossils do not have obvious living representatives. Fossils are usually fragmentary, however, and seldom consist of complete skeletons, or even parts of skeletons. All reconstructions of extinct life forms must be filtred through comparison with living forms, or by interpreting the conditions of fossilisation. Floral or faunal fossils found in the same strata as primate fossils can give a more detailed interpretation of the environment in which the animals lived and died. For example, a primate fossil found alongside a forest rodent or savanna rodent can give information on the primate's preferred habitat – closed or open, respectively – while fossil flora can provide information on the palaeoclimate that prevailed at the time – colder, warmer, wetter or drier (Bown et al. 1982; Krause and Bown 1993). The sedimentary sequence in which the organism was preserved (e.g., river or lakebed) can also provide insights into the animal's habitat, as well as ecological interactions between the organism and its environment. It may also influence the preservation process.

The distribution of fossiliferous deposits in time and space is dependent on many factors, the most important of which relate to the preservation of depositional environments, and the protection of the dead animals or plants from predation or dissociation and decay. As a result, fossil beds are sparsely distributed and limited across the African continent (see Figures 2.1 and 2.2, Table 2.4). Where they do occur, they are generally restricted to a limited time frame or sequence.

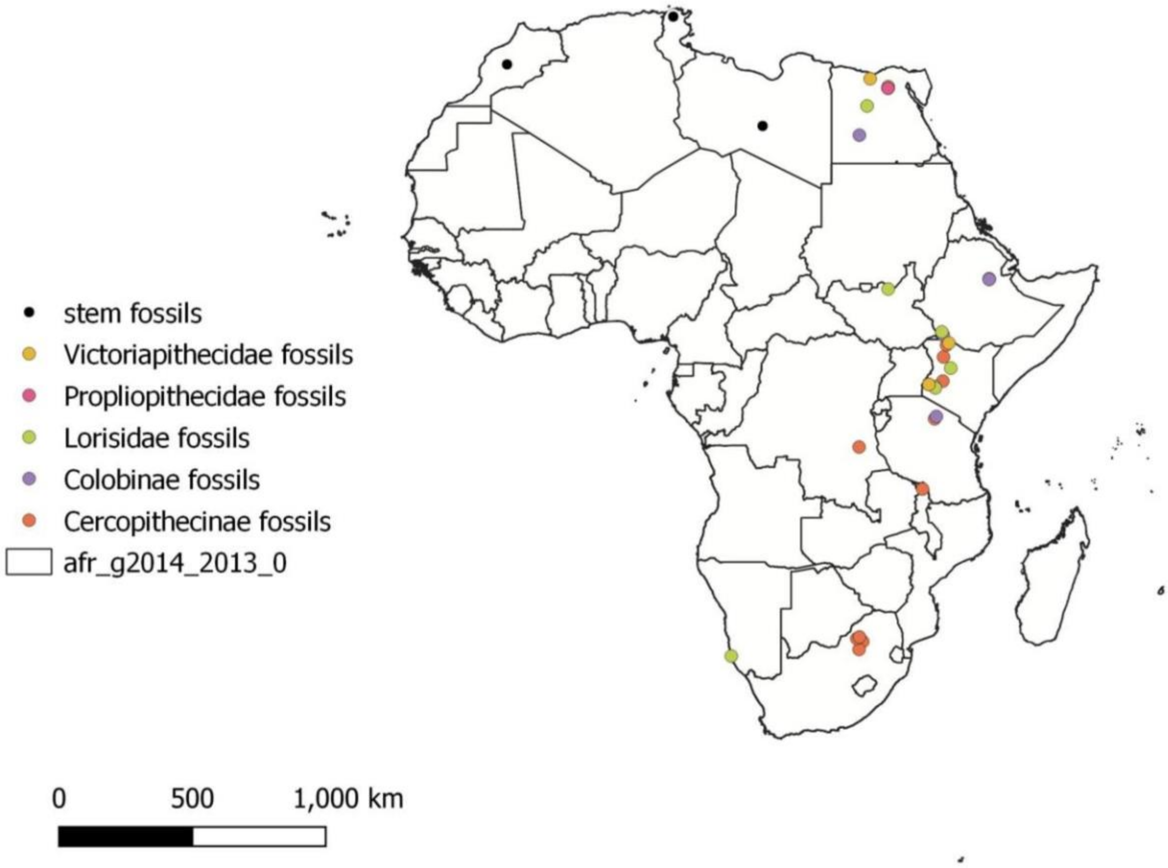


Figure 2.1. Map of Africa showing fossil sites from which non-human primates (colour-coded) have been recovered to date (data from various sources as described in the text).

The late middle Eocene site of Dur At-Talah in central Libya contains a diverse assemblage of stem primates (Figure 2.2), including strepsirrhines and haplorhines.

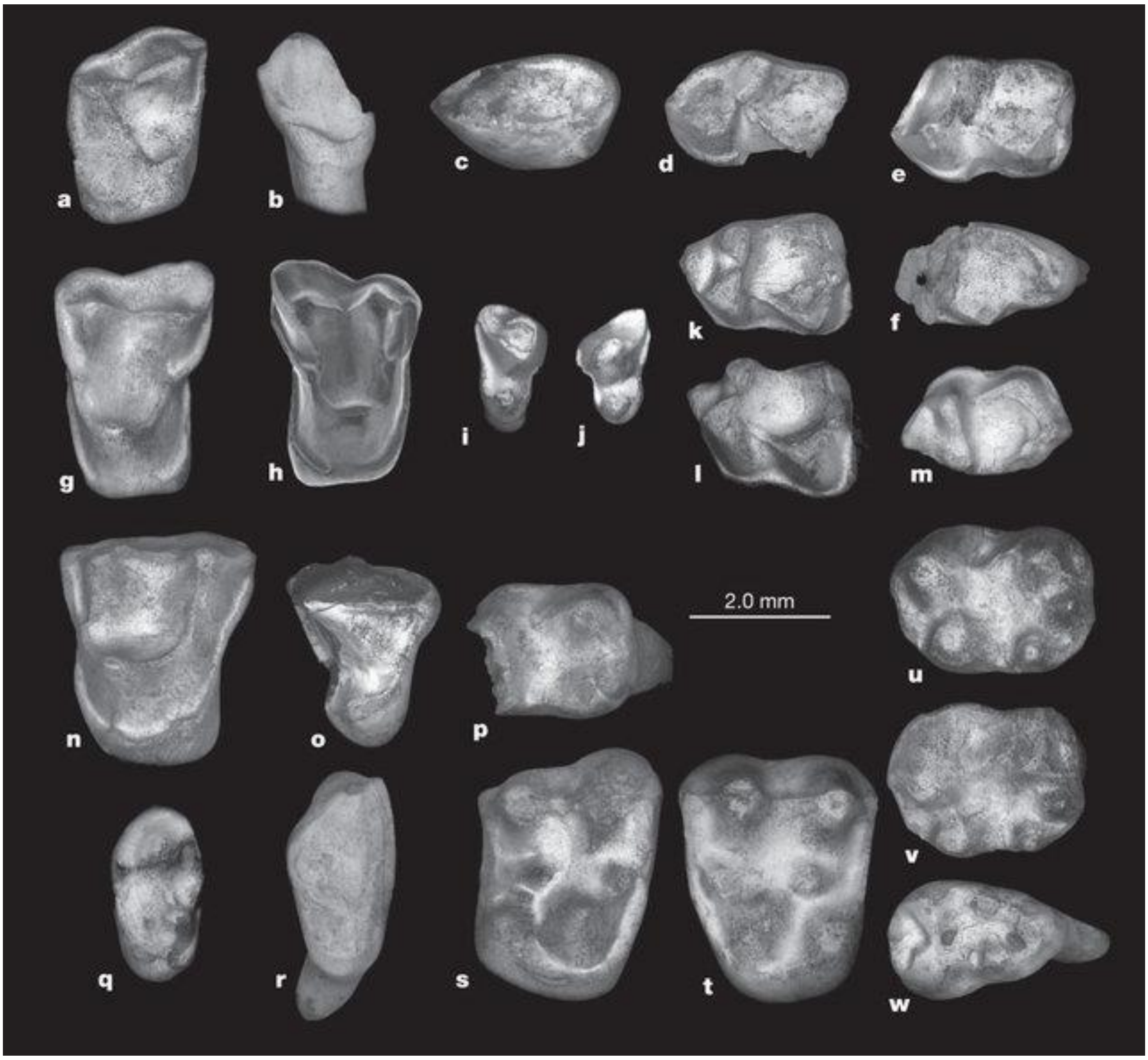


Figure 2.2. Stem primate fossils from Dur At-Talah, late-middle Eocene, central Libya (from Jaeger et al. 2010): teeth a-f represent a second species of the stem lorisoid genus *Karanisia*; g-m are attributed to a new species of the genus *Afrotarsius*, apparently related to modern tarsiers; n-p are accorded a new genus and species, *Talapithecus parvus*; q-w represent a new species of *Biretia.*

All of the fossil teeth are diminutive, suggesting that this deposit was a fissure filling (Jaeger et al. 2010). The stem lorisoid genus *Karinisia*, a strepsirrhine, was first discovered in late Eocene beds in the Fayum deposits of Egypt, and the older Libyan fossil has been assigned to a distinct species, *K. arenula*. Very few tarsiiforms are known from Africa. *Afrotarsius chatrathi* stems from Oligocene deposits (> 31 Ma) in the Fayum of Egypt (Simons and Bown 1985), while the Libyan taxon, *A. libyca*, is somewhat older. Two early simiiform taxa have also been recovered (Figure 2.1). They include a species of the parapithecid genus *Biretia*, known from the late middle Eocene in Algeria and the late Eocene in Egypt, and an entirely new genus of oligopithecid named *Talahpithecus parvus*.

Table 2.4. Summary of Africa's primate fossil record (see Figure 2.1 for sites location). Genus names in blue and purple are from North Africa; names in dark and light green are from East Africa; names in orange and red are from southern Africa. Darker shades denote genera affiliated with living taxa; paler shades have no known descendants.

Age (Ma)	Strepsirrhini	Haplorhini
Pleistocene 2.6 Ma – 10 ka	***Galago*** (1.5 Ma)	**(Hominini/Hominini)**
Pliocene 5-2.6 Ma	***Otolemur*** (3 Ma) ***Paragalago*** (3 Ma) ***Laetolia*** (4-5 Ma)	***Papio , Gorgopithecus*** (2 Ma) ***Theropithecus/Theropithecus*** ***Parapapio*** (4 Ma) **Colobinae** (4 Ma)
Miocene 23-5 Ma	***?Galago*** (10 Ma) ***Komba*** (19 Ma, 15 Ma) ***Mioeuoticus*** (19 Ma, 15 Ma) ***Propotto*** (19 Ma) ***Progalago*** (19 Ma)	***Chororapithecus*** (8 Ma) **Colobinae** (> 9 Ma) ***Samburupithecus*** (9.6 Ma) ***Nakalipithecus*** (10 Ma) ***Otavipithecus*** (13 Ma) ***Kenyapithecus*** (14 Ma) ***Victoriapithecus*** (20 – 15 Ma) ***Prohylobates*** (20 – 15 Ma) **Dendropithecidae** (20 – 15 Ma) **Proconsulidae** (20 – 15 Ma) **(Proconsulinae, Afropithecinae, Nyanzapithecinae)**
Oligocene 33.9-23 Ma	***Aframonius*** (33 Ma)	***Nsungwepithecus*** (25 Ma) ***Rukwapithecus*** (25 Ma) ***Aegyptopithecus*** (30 Ma) ***Propliopithecus*** (30 Ma) ***Parapithecus*** (30 Ma) ***Apidium*** (32 Ma) ***Moeripithecus*** (32 Ma)
Eocene 56-34 Ma	***Plesiopithecus*** (35 Ma) ***Wadilemur*** (35 Ma) ***Afradapis*** (37 Ma) ***Masradapis*** (37 Ma) ***Saharagalago*** (37 Ma) ***Karinisia*** (38 Ma) ***Namaloris*** (40 Ma) ***Notnamaia*** (~45 Ma) ***Namadapis*** (~45 Ma) ***?Algeripithecus*** (~48 Ma) ***?Azibius*** (~48 Ma) ***Djebelemur*** (50 Ma)	***Qatrania*** (33 Ma) ***Oligopithecus*** (33 Ma) ***Arsinoea*** (35 Ma) ***Catopithecus*** (35 Ma) ***Proteopithecus*** (35 Ma) ***Serapia*** (35 Ma) ***Afrotarsius*** (37 Ma) ***Biretia*** (37 Ma) ***Nosmips*** (37 Ma) ***Talahpithecus*** (38 Ma) ***Proteopithecus*** (40 Ma) ***?Algeripithecus*** (~48 Ma) ***?Azibius*** (~48 Ma)
Palaeocene 66-56 Ma		***Altiatlasius*** (57 Ma)

2.2.1 Palaeogene fossils (66-23 Ma)

Until recently, all African Palaeogene primate fossil sites were found within North Africa, i.e., Algeria, Egypt, Libya, Morocco and Tunisia, including the oldest known primate fossil, *Altiatlasius*, discovered in sedimentary deposits dated at 57 Ma in the High Atlas Mountains of Morocco. Both strepsirrhine and haplorhine fossils occur at these sites (Figures 2.1 and 2.2, Table 2.4). French palaeontologists, Senut and Pickford, changed this picture radically by discovering similar early Eocene fossils in Namibia. The limestones of the Sperrgebiet have yielded primitive adapiforms (*Namadapis, Notnamaia*) as well as a possible stem lorisoid (*Namaloris*) and an early simiiform (*Proteopithecus*) (Pickford 2015; Godinot et al. 2018). *Namaloris rupestris* is represented by a single upper molar, which has a similar shape to that of living lorisids (Pickford 2015), dated at approximately 40 Ma. The fossil was found among other animals such as rodents, as well as small Afrotherian animals (chrysochlorids, potamogalids and tenrecids) which form one of the oldest clades of living mammals.

Table 2.5. List of stem primate fossils found in Africa

Species	Stratigraphy	GPS degrees	Age	Reference
Altiatlasius koulchii	Morocco	31.7945, 7.0849	57 Ma	Sigé et al. 1990
Djebelemur martinezi	Djebel chambi	36.52, 9.3460	~50 Ma	Marivaux et al. 2013
Namaloris rupestrris	Sperregebiet Namibia	-27.367, 15.4549	~40 Ma	Godinot et al. 2018
Proteopithecus sylviae	Sperregebiet Namibia	-27.367, 15.4549	~40 Ma	Pickford 2015
Karinisia arenula	Dur At-Talah	25.715, 18.1819	38-39 Ma	Jaeger et al. 2010
Afrotarsius libycus	Dur At-Talah	25.715,18.1819	38-39 Ma	Jaeger et al 2010
Biretia piveteaui	Dur At-Talah	25.715,18.1819	38-39 Ma	Jaeger et al 2010
Talapithecus parvus	Dur At-Talah	25.715,18.1819	38-39 Ma	Jaeger et al 2010

Strepsirrhine fossils recovered in Africa include both stem galagids and lorisids, i.e., ancestral members of living lineages, as well as adapiforms, i.e., members of the extinct strepsirrhine infraorder. Galagos (Family Galagidae) and pottos (Lorisidae) have been living in Africa for at least 40 Ma. Teeth dated from the late Eocene (37-35 Ma: Seiffert et al. 2003; Seiffert 2007) that have been allied with these lineages, were found in the Fayum Depression in Egypt (Figure 2.1). These fossils include *Saharagalago* and *Wadilemur*, which are stem galagids, and *Karinisia*, which is a stem lorisoid. Fossils of the extinct adapiform subfamily Caenopithecinae have also been found in Eocene strata in Egypt. These include *Afradapis*, *Aframonius* and *Masradapis*. The latter genus was described recently by Seiffert et al. (2018), and consists of mandibular and maxillary fragments and isolated teeth. According to the authors' phylogenetic and biogeographic analyses, the common ancestor of caenopithecines migrated to Afro-Arabia from Eurasia between 49.4 and 47.4 Ma. *Plesiopithecus* is a unique fossil primate found in the Fayum beds, which has been linked to the Malagasy aye-aye (Godinot 2006; Gunnell et al. 2018). More recent fossils have been allied directly with living African lorisoid lineages. Tables 2.4 and 2.5 report lists of lorisoid fossils found in various sites in Africa.

Table 2.5. List of fossils of the superfamily Lorisoidea found in Africa

Species	**Stratigraphy**	**GPS degrees**	**Age**	**Ref.**
Namaloris rupestris	Sperrgebiet, Namibia	-26.675; 15.09	40 Ma	Pickford 2015
Karanisia arenula	Dur At-Talah	25.715; 18.1819	38 Ma	Jaeger et al. 2010
Karanisia clarki	Birket Qarun formation, Egypt	29.6; 30.6	37 Ma	Seiffert et al. 2003
Saharagalago misrensis	Birket Qarun formation, Egypt	9.6; 30.6	37 Ma	Seiffert et al. 2003
Wadilemur elegans	Jebal Qatrani formation, Egypt	29.5; 30.5	35 Ma	Gagnon 1997
Progalago songhorensis	Songhor, Kenya	-0.05; 35.2167	~19 Ma	Nengo & Rae 1992
Progalago dorae	Lake Victoria	-0.1833; 35.2579	~19 Ma	Harrison 2010
***Komba* spp.**	Maboko formation	0.166; 34.617	19 - 15 Ma	McCrossin 1992
***Mioeuoticus* spp.**	Napak, Uganda	2.35; 34.38	19 Ma	Leakey 1962
	Nachola site BG-K	1.78; 36.78	15 Ma	Kunimatsu et al. 2017
Galago farafraensis	Sheik Abdallah	27.69; 28.51	~10-11 Ma	Pickford et al. 2006
"Galago" sadimanensis	Laetoli, Tanzania	-3.0; 35.35	3.8-3.5 Ma	Harrison 2010
Otolemur howelli	Shungura formation, Omo valley, Ethiopia	5.36; 35.9	3 Ma	Wesselman 1984
***Paragalago* sp.**	Shungura formation, Omo valley, Ethiopia	5.36; 35.9	3 Ma	Wesselman 1984

The haplorhine primates from the Fayum included early simiiforms with three premolars (Parapithecidae, e.g., *Apidium*) and early catarrhines with two premolars (Propliopithecidae) like *Catopithecus* and *Aegyptopithecus*, which lived 33 Ma. Table 2.6 lists the propliopithecid taxa recovered from Oligocene deposits in the Fayum, all of which probably pre-date the ape – monkey divergence. The first record of this split is preserved in the latest Oligocene record of Tanzania (25.2 Ma), where two fossils, *Rukwapithecus fleaglei* (hominoid) and *Nsungwepithecus gunnelli* (cercopithecoid) were recovered from the same site (Stevens et al. 2013) (Table 2.4). Finally, the haplorhine infraorder Tarsiiformes has been in existence since 45 Ma in Eurasia (Beard 1998), and living forms are only known from Asia, but fragments of tarsier fossils (referred to *Afrotarsius*) have been found in Eocene deposits in Egypt, Ethiopia and Libya (Simons and Bown 1985; Jaeger et al. 2010).

Table 2.6. List of fossil species of the family Propliopithecidae found in North Africa

Species	Stratigraphy	GPS degrees	Age	Ref.
Talahipithecus	Dur At-Talah	25.715; 18.1819	38 Ma	Jaeger et al. 2010
Catopithecus browni	Jebal Qatrani	29.45; 30.5833	35 Ma	Gagnon 1997
Oligopithecus savage	Jebal Qatrani	29.45; 30.5833	33 Ma	Simons & Kay 1983
Propliopithecus haeckli	Jebal Qatrani	29.45; 30.5833	30 Ma	Simons 1965
Propliopithecus ankeli	Jebal Qatrani	29.45; 30.5833	30 Ma	Rasmussen & Simons 1988
Propliopithecus chirobates	Jebal Qatrani	29.45; 30.5833	30 Ma	Simons 1965
Aegyptopithecus zeuxis	Jebal Qatrani	29.45; 30.5833	30 Ma	Simons 1965

2.2.2 Early to mid-Miocene (23-15 Ma)

The primate fossil record for the first half of the Miocene epoch is preserved in East Africa, where the strepsirrhine genera *Progalago*, *Propotto*, *Komba* and *Mioeuoticus* have been found (Tables 2.4 and 2.5). Most of these fossils are fragmentary, but *Mioeuoticus* is represented by an almost complete skull (Figure 2.3). Although it was originally named after the living galagid genus *Euoticus*, *Mioeuoticus* closely resembles a lorisid (Phillips and Walker 2002; Harrison 2010).

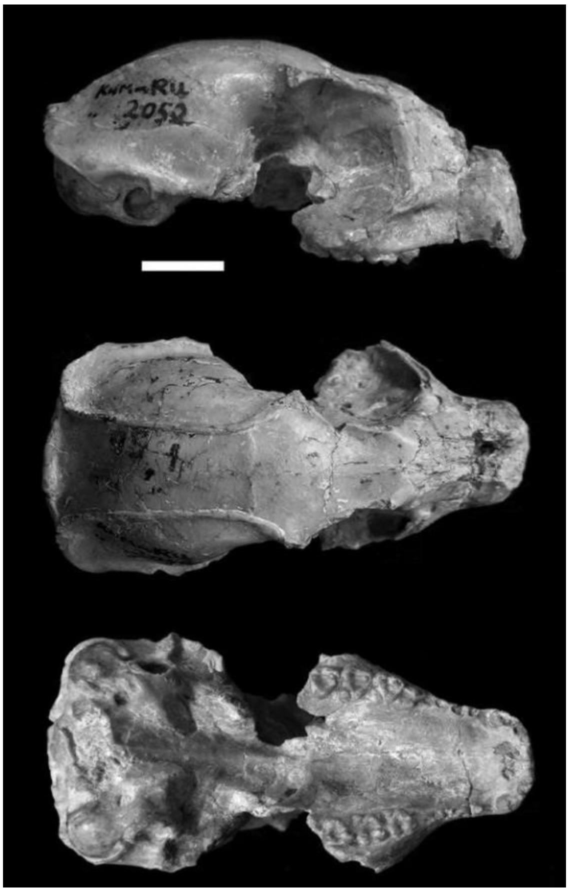


Figure 2.3. Cranial fossil of *Mioeuoticus shipmani* in lateral dorsal and ventral aspect (from Harrison 2010); white scale bar is 5 mm long.

Early Miocene haplorhines include two ape families classified within the superfamily Proconsuloidea: (1) Proconsulidae, with subfamilies Proconsulinae (1 genus, 6 species), Afropithecinae (5 genera, 5 species) and Nyanzapithecinae (6 genera, 8 species); and (2) Dendropithecidae (3 genera, 7 species). The proconsuloid apes are considered to be stem apes and catarrhines. While they share some characters with living apes (absence of a tail, skeletal characters; see Fleagle 2013), they cannot be allied directly with living African apes. In addition, at least seven largely monotypic genera of early African apes (7 genera, 8 species) are described from fragmentary material that has not been precisely allocated to particular families. Hence, during the early to middle Miocene, at least 22 genera and 34 species of apes inhabited Africa, whereas only 2 genera and up to 4 species (depending on the species concept used) are found on the continent today, and these are under threat of extinction.

Early fossils representing the superfamily Cercopithecoidea have been placed in a single extinct family, Victoriapithecidae (von Koenigswald 1969), named for *Victoriapithecus macinnessi*, which was found on Maboko Island, Kenya (Table 2.7). *Victoriapithecus* has been proposed to pre-date the divergence between the Colobinae (leaf-eating monkeys) and Cercopithecinae (cheek-pouched monkeys), possibly serving as an ancestor to both clades (Benefit and McCrossin 1993). The fossils found on Maboko Island were dated at > 14.7 Ma radiometrically, and < 16 Ma biostratigraphically (Benefit 1999), which corresponds to the Langhian stratigraphic stage (Table 2.3).

Table 2.7. Sample of Victoriapithecidae fossils found in Africa

Species	Stratigraphy	GPS	Environment	Age	Ref.
Nsungwepithecus gunneli	Nsungwe	-8.9; 33.45	Fluvial sandstone	25.2 Ma	Stevens et al. 2013
Prohylobates tandyi	Wadi Moghra	30.3811; 28.8203	Marginal marine sandstone	18 Ma	Fourtau 1918
Noropithecus bulukensis	Buluk	4.2667; 36.6	Coarse channel fill claystone sandstone	18 Ma	Harris & Watkins 1974
Victoriapithecus macinnesi	Maboko	0.166; 34.617	Wet floodplain	15 Ma	Benefit & McCrossin 1989

2.2.3 Mid- to late Miocene (15-5.33 Ma)

Mid- to late Miocene fossils have mainly been found in North and East Africa, although an important mid-Miocene site has also been discovered in the Otavi Mountains of Namibia (Figure 2.1). The only strepsirrhine fossils from the Late Miocene are fragments of galagids. Pickford et al. (2006) described *Galago farafraensis* on dental and postcranial remains recovered from the western desert in Egypt, and dated at 10 Ma. However, this date is much older than the divergence age of the genus *Galago* calculated using a molecular clock (Pozzi 2016), indicating that the fossil needs a new generic designation. Most primate fossils recovered from this time frame are haplorhine primates.

Conroy et al. (1992) discovered a mid-Miocene (13 Ma) fossil in Berg Aukas, central Namibia, which is a hominoid (*Otavipithecus*) of uncertain affinities. It consists of a right mandible that still retains most of its cheek teeth, the partial root of the canine, alveoli for all four incisors and a partial alveolus for the left canine. Four East African genera – each containing only one species – have been assigned to the family Hominidae: i.e., *Kenyapithecus*, *Samburupithecus*, *Nakalipithecus* and *Chororapithecus*, indicating their direct relationship to living African apes and humans. *Chororapithecus* was found in Chorora, Ethiopia, and dated at ~ 8 Ma (Katoh *et al.* 2016). It shares several characters with the living genus *Gorilla* (Suwa et al. 2007), and is postulated to have been an early member of this lineage.

The only Old World monkey fossils recovered from this time frame in Africa are colobines (Table 2.5). The oldest known genus is *Microcolobus*, dated to > 9 Ma, but other genera include *Kuseracolobus, Rhinocolobus, Dolichopithecus* (terrestrial), and

Paracolobus chemeroni (predominantly terrestrial). None of these fossil colobines can be allied with any of the living genera.

Table 2.8. List of Colobinae fossils found in Africa

Species	Stratigraphy	GPS	Age	Ref.
Paracolobus	Wash grp: Matabaietou formation	10.55; 40.5833	5-1.8 Ma	Vrba & Gatesy 1994
	Omo grp: Shungura formation	5.0639; 36.0361	2.5-1.8 Ma	Leakey 1982
Cercopithecoides	Kromdraai formation	-24.8; 27.75	4.82 Ma	Brain 1981
	Koobi Fora formation	4.067; 36.372	1.8 Ma	Harris 1991
	Olduvai Vogel River series	-2.9903; 35.3625	1.8 Ma	Leakey & Roe 1994

2.2.4 Plio-Pleistocene (5.33-0.01 Ma)

The majority of primate fossils from this time period have been found while excavating hominins. Most of the strepsirrhines recovered from these sites have been assigned to living genera: e.g., *Otolemur*, *Paragalago* and *Galago* remains from the 3 Ma Shungura formation in Omo (Wesselman, 1984; Harrison, 2010). *Galago sadimanensis*, described by Walker (1987) from 3.8 Ma old beds in Laetoli, Tanzania (Fig. 2.1), and 5 Ma old beds in Kapchebrit, Kenya, has since had a new genus created for it (*Laetolia*, Harrison 2011).

Haplorhine fossils from Pliocene beds (5.3-2.3 Ma) include several colobine monkeys (Boaz 1979) as well as species of the genus *Parapapio* from various sites in East and South Africa (Tables 2.8 and 2.9). Other papionin fossils include *Theropithecus oswaldi* with subspecies *T. o. oswaldi* and *T. o. leakyi.* Some of the *T. oswaldi* fossils recovered from the Konso formation in Ethiopia came from beds (i.e., the Sorobo and Turoha members) dated at ~1.9 Ma. A younger fossil was found in the middle part of the formation (the Kayle member), dated at ~1.6 Ma, and most of the *T. o. leakeyi* fossils were found in the Kayle and Karat members dated from ~1.45 Ma to ~1.25 Ma (Frost et al. 2014).

Table 2.9. List of Cercopithecinae fossils found in Africa

Species	**Stratigraphy**	**GPS degrees**	**Age (Ma)**	**Ref.**
Macaca libyca	Awash Grp-Adu-Asa formation	10.3167; 40.25	7 – 6	Kalb et al. 1982
Parapapio	Lothagam group	2.883; 36.067	7 – 2.5	Patterson et al. 1970
	Chiwondo formation Malawi	-10.167; 34	4 – 1.6	Bromage et al. 1995
	Kromdraai formation	-24.8; 27.75	2	Vrba 1975
Theropithecus oswaldi	Awash grp-Sagantole formation	10.6167; 40.5833	5.3 – 3.6	Kalb et al. 1982
	Traansval grp: Swartkrans	-6.0167; 27.7208	2	Brain 1994
Dinopithecus	Awash grp: Matabaietu formation	10.55; 40.5833	5.3 – 1.8	Vrba & Gatesy1994
Gorgopithecus major	Koobi Fora	4.067; 36.373	2.6 – 1.8	McDougall 1985
	Kromdraai	-24.8; 27.75	2	Brain 1981
Papio angusticeps	Malapa	-24.9523; 27.4918	2.3 – 2.2	Gilbert et al. 2015
Papio izodi	Taung	-25.238; 28.0852	2.2 – 1.8	Pickford 1988
	Laetoli	-3.2249; 35.1896		
Papio robinsoni	Swartkrans	-26.0189; 27.7163	2	Hartwig 2002
Papio anubis	Kapthurin formation	0.5; 36	0.3	Pickford 1988

CHAPTER THREE: REVIEW OF AFRICA'S MESOZOIC-CENOZOIC TECTONIC HISTORY

Earth consists of seven main tectonic plates, above and below sea level, which are constantly in motion: diverging and pushing away from each other, creating new ocean floors; converging or moving closer together, with the subduction of one plate under another; or passing each other along transform faults. These tectonic movements since 200 Ma have led to the fragmentation of Gondwana, with the separation of Antarctica-India, Madagascar and South America from Africa (Figure 3.1).

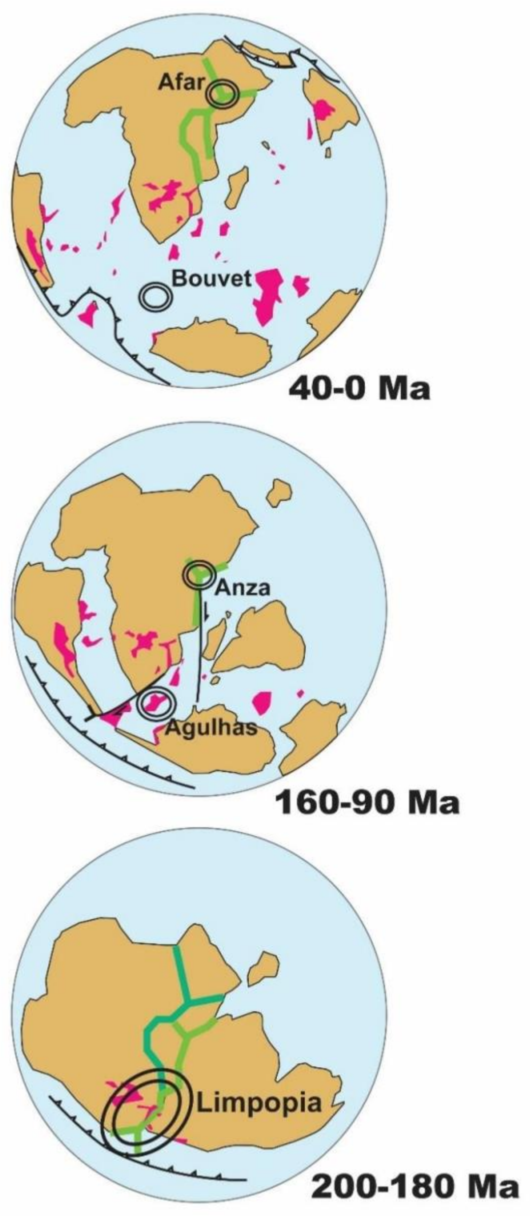


Figure 3.1. Fragmentation of Gondwana (from de Wit et al. 2020), showing successive episodes of rifting along the eastern margin of Africa: (bottom) 200-180 Ma, Early Jurassic; (middle) 160-90 Ma, Cretaceous; and (top) 40-0 Ma, late Cenozoic.

Rifting between west and east Gondwana began around 180 Ma, opening the Indian Ocean. Subsequent separation of South America and Africa and the opening of the South Atlantic began 130 Ma, followed by the opening of the Red Sea and East African Rift 40-20 Ma (Figure 3.1.). These continental movements have influenced the ocean circulation patterns and global climate, driving the formation of glaciers at the South and North poles from 34 Ma (Zachos et al. 2001). Polar glaciations in turn affected sea levels, and changed the erosional and depositional rates of rivers, streams and beaches. Together, these different surface processes have influenced the biogeography and evolution of plant and animal life on the different tectonic plates, and the climatic forces to which these faunas and floras have been subjected.

The Bouvet triple junction is a junction of three tectonic plates found on the seafloor of the South Atlantic Ocean, named after Bouvet Island, which lies 275 km to the east. The three adjacent plates are the South American, African, and Antarctic plates, separated by the Mid-Atlantic Ridge (MAR), the South West Indian Ridge (SWIR) and the South American Antarctic Ridge (SAAR). In contrast, the Anza trough is an isolated graben originating from East African rift-forming processes. It is not connected to the Bouvet (Limpopia; Figure 3.1) junction, but was possibly formed during the initial rifting of Gondwana. The separation of two other rifts from this junction allowed India-Madagascar to separate from Africa. The trough is now hidden by a cover of Pleistocene sediments and volcanic rocks across Kenya (Figure 3.2).

The formation of rift fractures drives magmatism and volcanism. Stress builds up over time until a weak zone is formed along a pre-existing fault, or a new fracture is created and basalts are erupted. The amount of volcanism is controlled by the rate at which the fractures open. At an opening rate of 1 mm/yr, no volcanism occurs; whereas at 1-10 mm/yr, alkaline or mildly alkaline basalts may be extruded; and at rates of 1-2 cm/yr, basalts of a transitional composition are extruded with secondary perialkaline silicics (Saemundsson 2010). Fissure eruptions may also occur depending on how much magma lies beneath them (Saemundsson 2010). Volcanoes have crustal magma chambers that outpour silicic magma, either in large volumes (known as pyroclastics) or in smaller flows (Saemundsson 2010).

In this chapter I describe the main continental rift systems of Africa using dates from the literature, and the various fossil sites in East Africa, which form the basis of this dissertation. My aim was to test spatio-temporal correlation between tectonism, volcanism and the evolution of African primates using phylogenetic reconstruction and the fossil record, as described in Chapter Five.

3.1 The Central African Rift System (CARS) 120- 50 Ma

The Central African Rift System (CARS) comprises Jurassic-Cretaceous basins that result from tectonic changes in the reorganisation of fragments from the African plate. The Anza and Sudan Basins form part of the NW-SE trending parts of the CARS, and occurred over a series of rifting events from the late Cretaceous to the Eocene-

Oligocene (Genik 1992; Bosworth 1992; Bosworth and Morley 1994; Morley et al. 1999a; Macgregor 2015). Apatite fission track analysis from surrounding basement outcrops (Foster and Gleadow 1996) and vitrinite reflectance data on the Elgal wells in Kenya (Bosworth and Morley 1994) show that the shoulders of the Anza rift were eroded by several kilometers during the late Cretaceous-Palaeogene period. This erosion cannot be seen today, but suggests that the original rift shoulders probably resembled the EARS shoulders of today topographically (Macgregor 2015).

3.2. The East African Rift System (EARS) 40- 20 Ma

The East African Rift Sytem (EARS) extends from the Red Sea and Gulf of Aden through the Afar region of Ethiopia, and southwards to Malawi (Figure 3.2) (Bonini et al. 2005; Chorowitz 2005). The Afro-Arabian Dome (4,550 m) covers an area of over 1,000 km^2 between the rifts of the Red Sea and the Indian Ocean ridge (Ebinger and Sleep 1998). The eastern rift is the third arm of the tectonic structure, which splits into two branches further south: one extending to the east and the other to the west. The oldest rocks formed from volcanism in Ethiopia and Kenya were alkali flood basalts, which erupted from depths of approximately 35 km, followed by saturated basalts, which are a cross between alkaline and tholeiitic eruptions from shallower depths. The final stage is observed in the Afar triangle, and formed by separation of the continental blocks and tholeiitic magmatism (Saemundsson 2010).

The eastern branch supports many volcanoes (e.g., Mount Elgon) centred around the Kenyan domal uplift, which spans a width of 1,000 km, and extends into the Indian Ocean. It breaks up further south into three arms, two of which form the main North-South section of the rift system, while the third, known as Kavirondo, extends westward from the centre of the dome (Figure 3.2). The western branch includes a number of deep lakes (e.g., Lake Victoria) but fewer volcanoes. It extends from the eastern edge of the Kenya dome, from Uganda to Tanzania and southwards to Malawi (Saemundsson 2010). Some of its rift basins contain hydrocarbon-filled sediments that are well dated.

The EARS is largely a product of geodynamic and magmatic activity initiated in the early to mid-Eocene (45-35 Ma). The South Lokichar basin began to form about 35 Ma (Vetel 1995; Macgregor 2015). The Loperot well descends through deep lacustrine shale dated securely at the Eocene-Oligocene transition (Morley et al. 1999b; Talbot et al. 2004; Macgregor 2015). Another lacustrine shale unit in the same area, the Lokone shale, is dated as early Miocene. This is overlain by the Auwerwer formation, a sandy infilling sequence from the mid-Miocene, which was uplifted to form part of the shoulder of theTurkana rift during the late Miocene-Pliocene (McDougall and Brown 2009; Macgregor 2015). The Turkana rift also connects to the South Kerio and North Lokichar rifts, which were initiated the during the early Miocene (Vetel 1995; Morley et al 1999a, b; Macgregor 2015). The northern Gregory Rift has an uplifted sandy section dated to early Miocene (20 Ma), the same date as the lacustrine deposits of Lake Turkana (Bosworth and Maurin 1993; Ebinger et al 2000; Macgregor 2015).

The Gatome and Lotikipi rifts continued extending from the Anza Graben from the Palaeocene to the early Miocene periods (Wescott et al. 1999; Macgregor 2015). Recent stratigraphic studies (Macgregor 2015; Delauney, 2018; Guillocheaud et al. 2018; Masters et al. 2021) thus point to three major uplift periods of the EARS during the Cenozoic: in the early Palaeogene; from the Eocene-Oligocene boundary to the early Miocene; and ongoing activity since the mid-Miocene. These phases also led to the current topography of Madagascar (Figure 3.2).

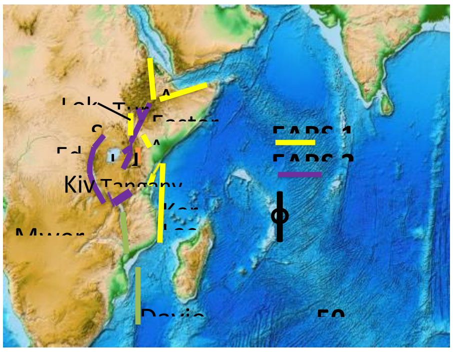


Figure 3.2. Digital elevation model (Etopo) of the East African Rift System (EARS). The short orange line depicts Cretaceous and Palaeogene rifting, while the yellow lines highlight rifts that occurred from the Oligocene to the mid-Miocene. The purple lines indicate later rifting that took place after the mid-Miocene.

The Gregory Rift does not indicate pre-existing rift topography, suggesting that the western branch of the EARS did not proceed further south (Morley et al. 1999a; Wichura et al. 2010, 2011; Macgregor 2015). Rifting in Ethiopia occurred mostly in the southern part of the country (Bonini et al. 2005), beginning 25-21 Ma, and becoming evident by 17-15 Ma (Levitte et al. 1974; Zanettin et al. 1978; Ebinger et al. 2000; Macgregor 2015). The western branch is made up of a sandy section within the Rukwa Basin dated as Oligocene (Roberts et al. 2010, 2012; Macgregor 2015). The Sungwe beds of Malawi are also thought to be of this age by correlation (Dixey 1927; Macgregor 2015). The western branch shows evidence of low levels of tectonic activity and volcanism around 10 Ma, with small exceptions from the Rungwe complex occurring in the early Miocene (20 Ma; Kampunzu et al. 1998; Rasskazov et al. 2003; Macgregor 2015). The eastern branch stretches from the Afar region of Ethiopia to northern Tanzania with no break points (Ebinger and Sleep 1998; Macgregor 2015).

Rifting of the EARS is faster at the northern extremity, where it began, slowing towards the south. In the Red Sea, rifting occurs at a rate of 2.6 cm/yr; in the Afar region, the rate is 1 cm/yr; in the Ethiopian Rift, it is estimated at 0.7 cm/yr; and in the eastern and western wing of the Kenya dome, 0.5 mm/yr (Saemundsson 2010). Doming, rifting and alkaline magmatism (volcanism) are related to the events that led to the formation of the EARS, which experiences shallow earthquakes: shallowest in the Afar region and deepest in the southernmost area (Saemundsson 2010). The western part of the EARS is presently more active than the eastern part, and studies show normal faulting (Kebede and Kulhánek 1991; Stamps et al. 2008; Saemundsson 2010).

Four magmatic phases have taken place since the mid-Miocene, beginning with melting of the upper mantle, causing the first gradual uplift. This led to more intense melting of the uppermost mantle and lower crust, creating phonolites during the late Miocene, and finally, melting of the lower crust caused by the lowering of the central rift, leading to the release of trachytes (Bailey 1974; Saemundsson 2010).

Macgregor (2015) used several techniques to characterise the rifting events:

1. biostratigraphic and volcanic dating within well penetrations, tying them to seismic data whenever possible;

2. biostratigraphic or volcanic dating of exhumed outcrop sections of rifts;

3. dating volcanic outcrops and analyses of their thickness in relation to rift-bounding faults;

4. extrapolation of measured sedimentation rates to a mapped basement horizon;

5. correlations of intervals of similar seismic character between sedimentary basins;

6. labelled seismic correlations within investors' presentations that could not be fully audited because of their confidential nature.

Using these techniques, geological age reconstructions achieve a resolution varying between about 10 and 1 Ma. Macgregor (2015) estimated that the Rwenzori Mountains, Earth's highest non-volcanic, non-orogenic mountains, were uplifted during the Plio-Pleistocene from the folding of Pliocene strata (Senut and Pickford 1994; Pickford et al. 2004). Flora and fauna from the Kingfisher wells in the Albertine basin, which flourish at high altitude, are as recent as 1 Ma (Shaw et al. 2009; Macgregor 2015). Based on the dating and measurement of volcanic outcrops (technique 3 of the above list), Macgregor (2015) concluded, in agreement with Baker (1986) and Dawson (2008), that the Gregory Rift shoulders only rose 1-2 Ma (Table 3.1).

Table 3.1. Summary of rifting dates within the East African Rift System (see Figure 3.2 for locations) as estimated by Macgregor (2015). Estimated periods of rifting are colour-coded as follows: Eocene-Oligocene (cerise); early Miocene (yellow); mid-Miocene (green); late Miocene (blue); Plio-Pleistocene (grey).

Western branch	**Age of rifiting**	**Eastern branch**	**Age of rifting**
Lake Albert	16-0 Ma	Central Main Ethiopian Branch	31-26 Ma 18-17.5 Ma 16 Ma 14-13.8 Ma 12 Ma 11.6-9 Ma 8-0 Ma
Lake Edward	5-0 Ma	Southern Main Ethiopian Branch	>40-38.5 Ma 38-32 Ma 22 Ma 21 Ma 20 Ma 20-11.5 Ma 5-0 Ma
Lake Tanganyika	12-0 Ma	Omo and Turkana	36-23 Ma 21-20 Ma 19-18 Ma 17-0 Ma
Lake Rukwa	5.3-0 Ma	Lokichar	31-0 Ma
Lake Malawi	7.2-0 Ma	Northern Gregory	21-18 Ma 16-11 Ma 10-0 Ma
		Central Gregory	23 Ma 20-16 Ma 14-11 Ma 7 Ma 5-0 Ma
		Southern Gregory	6 Ma 5 Ma 4 Ma 3 Ma 2.6-0 Ma
		Tanzanian Rift	8 Ma 4-0 Ma

Table 3.1 summarises the major rifting events that generated the East African Rift System (EARS) as estimated by Macgregor (2015). The first column lists locations within the western branch, while the second column gives the ages of rifting at these locations. The third lists areas within the eastern branch, and the fourth column gives

the estimated ages of rifting in that area. The rift localities are arranged from north to south, and time intervals for the rifting events are highlighted in different colours. The colour-coding shows two facts at a glance: (1) the oldest tectonic events occur only in the eastern branch of the rift; (2) the pattern of timing of tectonic events is complex, but older events are generally located further north than more recent rifts.

Many primate fossils have been found within the EARS, which includes exposures covering much of African primate history, including fossils of the focal primates of my study who still live in the region today (Figure 3.3). Divergence and diversity of galagids, monkeys, baboons and hominids are likely to have been influenced by the development of this extensive rift system, in terms of both space and geological time.

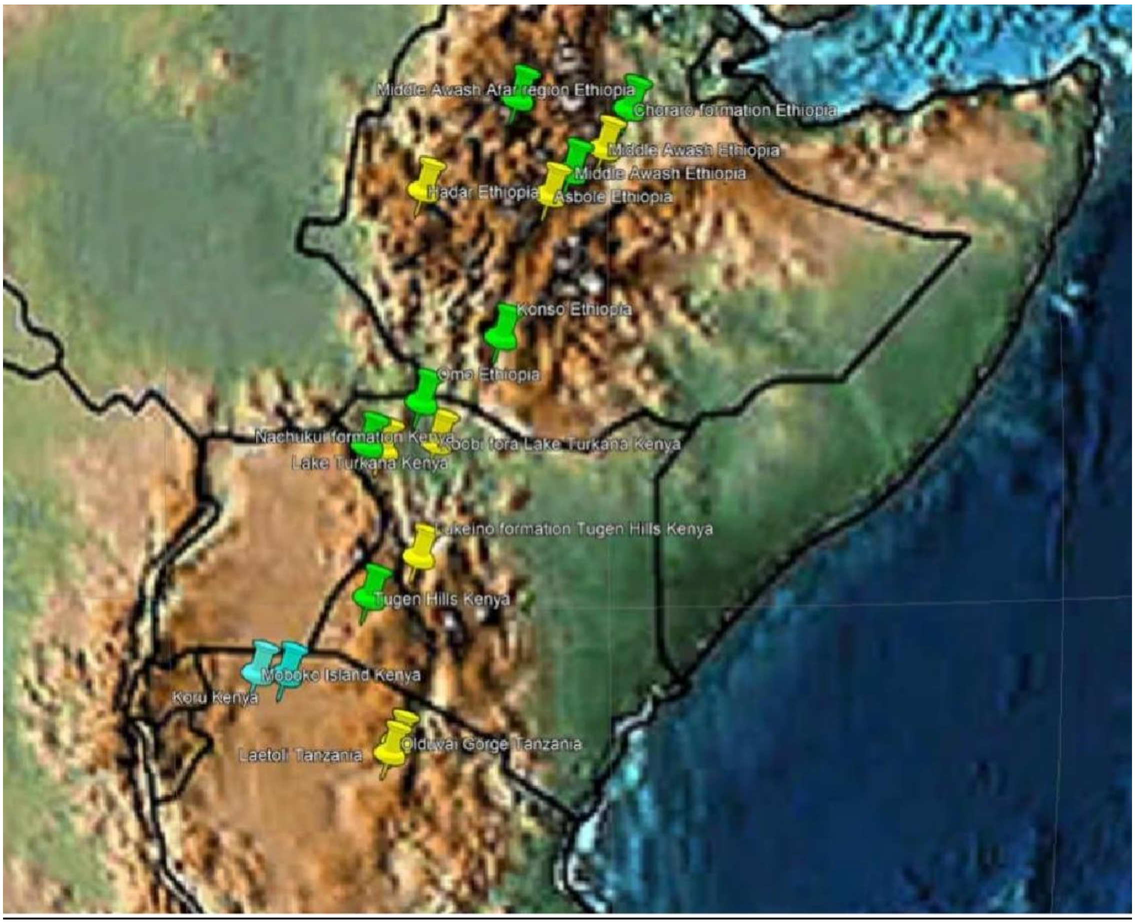


Figure 3.3. Map showing the sites of primate fossils found within the East African Rift System, and stemming from different time periods. Sites dated between 23.03 and 15.97 Ma are represented by blue pins; those from 11.63 to 5.33 Ma are shown by green pins; and those dated to 5.33-0.0017 Ma are noted by yellow pins (see text for a detailed description).

3.3 Fossil sites in the East African Rift System

3.3.1. Ethiopia

The main Ethiopian rift begins in the central Afar depression ~11.5°N, where it forms part of the Red Sea-Gulf of Aden-Ethiopian triple junction (Figure 3.2). Within the Afar depression, large areas of land are below sea level (Corti 2009). The Ethiopian rift is magmatic, forming the boundary between the Nubia and Somalia plates. It extends 1,000 km, trending NE-SW from Afar south to the Turkana depression. The majority of fossils found in Ethiopia, including hominins, were recovered within the Afar Triangle, which is traversed by the Awash River. Remains of *Ardipithecus* species, dating from 5.8 to 4.4 Ma, were recovered from the Middle Awash Valley (Haile-Selassie et al. 2004). Hadar, the site of the discovery of 3.2 Ma old "Lucy", the 40% complete skeleton of an *Australopithecus afarensis* female (Johanson et al. 1982), is located at the southern edge of the Afar Triangle. The Bourie formation, which yielded the 2.5 Ma *Australopithecus gahri* and early stone tools, is also in the Middle Awash Valley (Asfaw et al. 1999). The Omo River in southern Ethiopia is the provenance of the oldest known skeleton of *Homo sapiens* (Pearson et al. 2008).

3.3.2. Kenya

The Ethiopian Rift links to Lake Turkana in north-western Kenya, which is the site of several hominin fossils, including the Nariokotome boy, a near- complete skeleton of an 11-year-old *Homo ergaster* boy who died 1.5 to 1.6 Ma ago, and was discovered by Kimeu (Walker and Leakey 1993). Further south in Kenya, the Tugen Hills fossil site is located in the Gregory Rift, west of Lake Baringo (Figure 3.3). The hills extend 100 km N-S, and their highest point is 2,400 m on the Saimo Horst. The 3 km thick volcaniclastic and sedimentary succession of the Tugen Hills forms one of the most complete Neogene records in Africa. Tectonic subsidence during the Miocene led to lithostratigraphic units that are either lacustrine or fluvial. In the Pliocene these were uplifted by volcanism and are now outcropping. The Tugen Hills yielded the remains of *Orrorin tugenensis*, a potentially bipedal hominid (Senut et al. 2001).

3.3.3. Tanzania

Mahenge is a middle Eocene locality in Tanzania. Plant fossils found in lacustrine deposits associated with a crater-lake resemble the elements that make up modern miombo environments, which occur there today. The site has also yielded frog and fish fossils and a few mammal fossils (Jacobs 2004). Among the plant assemblages are legume species (Fabaceae), some of which are ceasalpinoid (Herendeen and Jacobs 2000). There are also mimosoid species that include the earliest record of the genus *Acacia*, which should now be referred to *Senegalia* or *Vachellia*. Graminoid impressions could represent aquatic grasses, ground cover or both. Rainfall reconstructions from regression models of modern low-latitude leaf and rainfall data are equivalent to 600 mm/yr, but during the Eocene the dry season was probably less severe than today (Jacobs 2004; Jacobs and Herendeen 2004).

The Eyasi Plateau includes three fossil localities: Kakesio, Esere-Noiti and Laetoli (Figure 3.3) (Foster et al. 1997). The last is most widely known because of the many fossils found there, including the famous 3.6 Ma hominin footprints (Leakey and Hay 1979). Laetoli is on the southernmost part of the eastern branch of the EARS, and its past vegetation ecology has been reconstructed as wooded grassland by Andrews and Bamford (2008). The sedimentary sequences are exposed along the border of the Eyasi Plateau that separates Lake Eyasi and the Olduvai Gorge basin (Kent 1941). The site spans an area of more than 1,600 km^2 although most fossils derive from an area of ~100 km^2 along the Garusi River. The site comprises fault blocks forming the central graben, with plateaus forming the sides of the lake basins. The Laetoli deposits are tuffs spread over Precambrian basement; the Ngorongoro volcanic highlands overlie the deposits to the east. The two lithological units have been K-Ar dated, and cover the periods 4.3-3.8 Ma (lower unit) and 3.8-3.5 Ma (upper unit). A series of calcretes and tuffs – the Ndolanya beds – overlie the Laetoli beds. Fossils from the upper Ndolanya beds have been radiometrically dated to ~2.6 Ma. The beds are capped by the 2.41 Ma Olgal lavas (Kingston and Harrison 2007).

Olduvai Gorge is located 2-4°S, 34-36°E in the eastern branch of the EARS. The area includes the Serengeti Plains (1,500-1,800 m elevation), the Crater highlands and Lakes Eyasi, Manyara and Natron. The Crater highlands reach 3,050 m a.s.l., and stretch SSW-NNE, creating a rain shadow over the eastern Serengeti Plains. Olduvai Gorge comprises a series of 100 m thick deposits, inluding lacustrine, fluvial, aeolian and pyroclastic sediments, deposited ~1.92 to ~0.2 Ma in a closed-basin saline lake. The archaeological sites were dated using tuff horizons (Barboni 2014).

The Ngorora formation consists of a sequence of tuffaceous beds with interleaved fluvial or lacustrine siliciclastic deposits and paleosols. Deino and Potts (1990) used three methods to date this formation at 13.1 – 7.8 Ma. The first used single-crystal $^{40}Ar/^{39}Ar$ dates from the uppermost flows of the Tiim phonolites; the second involved single-crystal $^{40}Ar/^{39}Ar$ ages from tuff and lapilli- bearing sediments; and the third used K-Ar dates from the Ewalel phonolites that overlie the formation. Many terrestrial (mammals, insects) and some aquatic (fishes, turtles, crocodiles, ostracods) fossils have been found in this formation, as well as plant fragments, fossil leaves and fruits dated at 12.6 Ma. A second site, called Waril, is slightly younger (10 Ma), according to the lithostratigraphy.

3.3.4. Malawi

The northern Malawi Rift (Ring and Betzler 1995) has yielded hominin fossils. A hominin mandible, referred to *H. rudolfensis*, was discovered at Uraha, Malawi (HCRP-UR 501) in sediments of the Chiwondo beds, dated at 2.5-2.3 Ma (Schrenk et al. 1993). More extensive excavations at the Uraha and Malema sites also yielded remains of *Paranthropus boisei*, a “robust” australopith (Kullmer et al. 1999), indicating that the two taxa coexisted in this area (Figure 3.3).

CHAPTER FOUR: AFRICA’S PALAEOCLIMATIC HISTORY

The influence of climate changes on vegetation and habitats is well known, particularly given the accelerated global warming of the Anthropocene, which offers measurable evidence of these effects. Changes in habitats, in turn, generate forces of natural selection for animals and plants, because populations that evolved under one set of conditions are less adapted to the new temperature and rainfall regimes, as well as new food sources and predator guilds. Today Africa comprises 3 climatic regions receiving less than 200 mm of rain annually (Couvreur et al. 2021). In order to understand these interactions, it is necessary to explore scientific interpretations of past climates and their corresponding vegetation, particularly across where hominins first emerged during the Cenozoic.

4.1. Methods of understanding palaeoclimates

4.1.1. Faunal reconstructions

Palaeontological studies of terrestrial environments use the presence of mammals in fossil beds to infer the relative openness of the habitat. Large mammals – especially bovids – provide most of the information for palaeoecological reconstructions after the mid-Miocene period, when open grassland habitats spread. They do not provide irrefutable evidence of open landscapes, however, because some extant close relatives occupy both open and closed environments; e.g., African elephants have populations in both forests and acacia woodlands; Cape buffaloes occur mainly in woodland savannas, but forest buffaloes also occur in the rain forests of West Africa. Megaherbivores play an important role in creating open habitats by their activities (Owen-Smith 1988), but their fossils are not abundant.

The Alcelaphini (wildebeest, hartebeest, bontebok clade) and Antilopini (gazelle and springbok clade) are the most common fossil taxa used to identify open and seasonally arid environments (Bobe 2006). Antilopines include both browsing and grazing species. The browsers tend to occupy drier or arid environments, where leaves from bushes contribute an important part of their diet. They are hence indicative of mosaic bush-grassland habitats. Alcelaphines are grazers, indicative of grasslands. In contrast, the Hippotragini (roan, sable, oryx clade) occupy a range of habitats, from grassland to woodland and desert, all with seasonally arid conditions. Other grazing bovids such as the Reduncini (reedbuck, lechwe, kob, waterbuck) and Bovini (buffalo) live in waterlogged areas or woodlands (Bobe 2006).

4.1.2. Palaeobotanical and palynological reconstructions

In addition to using the presence of large mammal fossils to infer palaeoclimates, the study of fossil plants and pollen (i.e., palaeobotany and palynology) can provide more direct information regarding the palaeoclimate of a region.

Plants can use one of two photosynthetic pathways, C_3 or C_4, named for the number of carbon molecules present in the carbon product that is produced by the process. Plants with C_3 pathways emerged during the Palaeozoic and Mesozoic eras, 500 to 200 Ma, and include the most common grasses alive today, making up 95% of global plant biomass. C_3 grasses are more likely to be found in humid climates with lots of soil moisture. In contrast, C_4 grasses emerged much later during the Miocene, 20-15 Ma. They are able to handle extreme conditions such as drought, high temperatures, and low CO_2 and nitrogen concentrations, and they thrive in hot, dry climates. They dominate the tropical and subtropical regions, making up 90% of all savannas and grasslands (Keeley and Rundel 2005). By identifying the carbon fixation pathway of fossil plants, researchers can interpret the temperature, rainfall and light availability of the environment within which they grew, as well as their latitude, although C_4 and C_3 plants are able to grow within close range of each other when soil moisture and shade allow (Albert et al. 2015).

4.2. The Cenozoic record of African climate and vegetation

The transition from the Cretaceous to the Palaeogene was marked by a major mass extinction at 66 Ma (Alvarez et al. 1980). During the Palaeocene epoch, when the two major living lineages of primates, the Haplorhini and Strepsirrhini, apparently diverged (Perleman et al. 2011; Springer et al. 2012), the global temperatures increased steadily, and reached a maximum during the latest Palaeocene and the early Eocene, around 56 Ma (Figure 4.1). The Palaeogene record of Africa had a heterogenous flora; although most parts were forest and woodland, there were also areas covered entirely by grassland (Morely 2000; Bobe 2006), suggesting more arid conditions compared to the present.

4.2.1. The Palaeocene-early Eocene Thermal Maximum (66-56 Ma)

Fossil plant and isotope records from around 56 Ma indicate that this was the warmest episode during the Cenozoic (Wolfe 1994; Wing 2000; Zachos et al. 2001; Jacobs and Herendeen 2004). Gutjahr et al. (2017) proposed that this global warming was driven by volcanism. Low ocean surface pH values and the carbon isotope record suggest that the major cause of the late Palaeocene-early Eocene Thermal Maximum (PETM) was volcanic eruptions within the North Atlantic Igneous Province. The Eocene epoch in the northern hemisphere was wet and warm, and the northern continents were covered by broad-leaved forests (Wolfe 1994; Wing 2000). During this time period, haplorhine and strepsirrhine primates radiated extensively in North America and Eurasia (Fleagle 2013). Based on the fossil primates recovered from North Africa, Libya and Egypt (Figure 2.1) were likely to have been forested during the Eocene.

The Eocene climate of southern Africa appears to have been much drier. The Mahenge palaeontological site in Tanzania is an ancient crater-lake deposit that formed on top of kimberlite dated as mid-Eocene (46 Ma) using $^{206}Pb/^{238}U$

geochronology of zircon (Mannard 1962; Herendeen and Jacobs 2000; Jacobs and Herendeen 2004). The flora and fauna excavated at the site suggest that the area had mean annual precipitation values around 660 mm/year. For comparison, a modern forest environment would require 1100 mm/year. These different Eocene climatic conditions may have been related to the absence of the Tibetan Plateau, which controls monsoon circulation today (Lockwood 1986; Ruddimann and Kutzbach 1989; Prell and Kutzbach 1992; Zhisheng et al. 2001; Jacobs and Herendeen 2004).

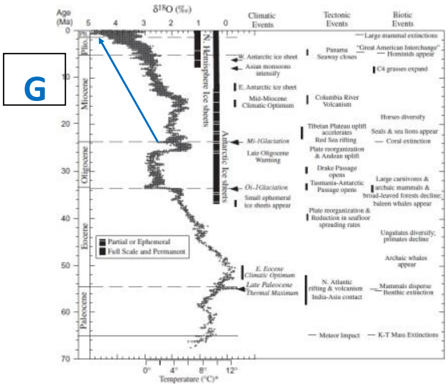


Figure 4.1. Representation of Cenozoic climate based on ∂^{18}O measured from marine nanofossils, and biotic and tectonic events based on geological and palynological records (Zachos et al 2001). Note the general decreasing trend in temperature due to the installation of Polar ice sheets since the Oligocene (blue arrow).

The Palaeocene-Eocene Thermal maximum coincided with a major extinction of foraminifera, and lasted approximately 100,000 years (Gingerich 2006). The event was also characterised by a negative carbon isotope excursion (Koch et al. 1992), an indicator of global climate change. During this period, ^{13}C dropped by 2.5‰ caused by additional mixing of ^{12}C in the ocean and atmosphere.

In the Eocene, woodland habitats occurred close to the Tethys seaway (Guinet et al. 1987; Maley 1996; Bobe 2006), as well as in Mahenge, Tanzania, which was possibly wooded as early as 46 Ma (Herendeen and Jacobs 2000). The mid-Eocene African woodland would have been similar to the miombo woodland that currently covers large areas of sub-Saharan Africa, causing the spread of more arid-adapted fauna and vegetation that could survive such conditions (Potts and Behrensmeyer 1992; Wing and Sues 1992; Bobe 2006).

4.2.2. The Eocene-Oligocene transition (34 Ma)

During the late Eocene, marine temperatures dropped by 4°C (Figure 4.1), decreasing even further at the Eocene-Oligocene boundary, with the formation of ephemeral ice sheets in the Antarctic (Lear et al. 2000; Zachos et al. 2001; Coxall et al. 2005; Bobe 2006). In Egypt, the Fayum deposits show the occurrence of mangroves during this cooling event (Bown et al. 1982; Bobe 2006), indicating that North Africa was also relatively moist at that time, while the inland parts of the continent were possibly drier (Jacobs 2004; Bobe 2006).

4.2.3. The Miocene (23-5.3 Ma)

The early Miocene (18-14 Ma) was marked by a slight warming period after the Oligocene epoch (Figure 4.1). During this interval, terrestrial environments in Ethiopia, Kenya and Uganda were wooded and forested, although there is evidence of some grasslands along with the woodlands in Kenya (Shipman et al. 1981; Miller et al. 1987; Retallack et al. 1990; Cerling et al. 1991; Zachos et al. 2001; Bobe 2006). Southern Africa may have become more arid during the mid-Miocene owing to the Benguela current and the upwelling of its cold waters (Siesser 1978; Sègalen et al. 2004; Udeze and Oboh-Ikuenobe 2005; Bobe 2006). According to oxygen isotope records from the South Atlantic Ocean, there was a period of significant cooling at 12.5-5.5 Ma, closely followed by polar glaciations between 10 and 6 Ma, which led to the expansion of tropical grasses and sedges (C_4 vegetation) in Africa (Ring 2018). Jacobs and Kabuye (1987) demonstrated that the Baringo basin of the Kenyan Rift had a tropical moist climate at 15.5-12.5 Ma, which was characterised by C_3 vegetation. Fossil plants from three sites revealed that this area was covered with lowland to sub-montane forests. Rainfall has been estimated to 1,000-1,200 mm/yr, higher than today (900 mm/yr). Bonnefille (2010) predicted similar vegetation changes in the Gulf of Aden at 12-11 Ma. By 10-9 Ma, plant fossils indicate the presence of more grassland ecosystems, with rainfall estimated around 500-700 mm/yr. The greatest amounts of grass pollen were recovered from layers dated at 10.5 Ma and 7 Ma (Bonnefille 2010; Rasmussen et al. 2017). Plant fossils from a site dated at 7.2-6.8 Ma indicated a woodland environment with an average rainfall estimate of 900-1,000 mm/yr. Between 8 and 5 Ma, there was another significant change in the biota, with the expansion of C_4 grasslands in East Africa (Jacobs et al. 1999). This is recorded in fossil data from elephantids and equids, which shifted from a mostly C_3 to a mostly C_4 diet around 8-7 Ma. Tree pollen abundance decreased from 7 Ma and reached its lowest level at 6.5-6

Ma (Bonnefile 2010). By the late Miocene, aridity was well established across Africa (Cerling et al. 1993, 1997; Morley and Richards 1993; Morgan et al. 1994; Bobe 2006), peaking around 5 Ma in the Kenyan part of the EARS. This peak coincided with the Messinian salinity crisis (5.9-5.5 Ma), which apparently affected climate on a global scale. Today, the rainfall regime in tropical Africa varies longitudinally with the western monsoon region and and the western Congo basin being far wetter than the margin of the continent east of the East African and Ethiopian domes (Couvreur et al. 2021)

4.2.4. The Pliocene (5.3 – 2.6 Ma) and Pleistocene (2.6 Ma – 10 ka)

During the last 5 Ma, global surface temperatures decreased by 3°C to today's levels (Ring 2018). Rain forests were present in parts of East Africa (Williamson 1985; Pickford et al. 2004; Bobe 2006), although the Sahara experienced increasing aridity 3-2 Ma (Dupont and Leroy 1995; Morely 2000; Bobe 2006). Data retrieved from carbon palaeosols in the Turkana basin show three peaks of C_4 vegetation, and thus aridity, at 3.6, 2.5 and 1.8 Ma (Wynn 2004; Bobe 2006). Although grasslands expanded in the late Miocene, the landscapes similar to today only became more commonplace during the Plio-Pleistocene (Cerling et al. 1988; Kingston et al. 1994; Bobe and Behrensmeyer 2004; Bobe 2006). When large African mammals (e.g., Proboscidea and Embrithopoda) evolved in the Palaeogene, the African continent was separated from Eurasia by the Mediterranean Sea. Megaherbivores probably played an integral role in creating a more heterogenous, open landscape, which was driven by climatic and tectonic changes of the EARS (Owen-Smith 1988; Partridge et al. 1995; Herendeen and Jacobs 2000; Bobe 2006).

The forests of East Africa were separated by an arid corridor from the Central African rain forests, which stretched from the northeast to the southwest on the coast of Namibia. The corridor is dated to the Miocene (Bobe 2006), and is thought to have been the place where the spread of C_4 grasslands occurred at 6 Ma, 3 Ma, and 2 Ma (Sègalen et al. 2007). There was not a single event, but rather a gradual shift involving reversals between arid and humid episodes, along with changes in the periodicity and amplitude of climatic oscillations (Figure 4.1). Another factor that influenced the African climate relates to marine oxygen isotopic records, which show that high latitude sea-surface temperatures, ice rafting and deep circulation varied significantly at 5 Ma (de Menocal 2004). According to data derived from aeolian dust extracted from marine sediment cores from West Africa, East Africa and Arabia, the changes in African climate coincided with changes in high latitude climates (de Menocal 2004). The expansion of grasslands in the Pleistocene resulted in the extinction of large specialised mammals in favour of smaller, more generalised counterparts (Table 4.1, Figure 4.2).

Table 4.1. Table showing presence (=1) or absence of large herbivorous mammals (> 350 kg) from the onset of the Miocene to the Holocene, adapted from Bobe (2006)

Megafauna	**Early Miocene**	**Middle Miocene**	**Late Miocene**	**Pliocene**	**Early Pleistocene**	**Middle Pleistocene**	**Late Pleisocene**	**Holocene**
Gomphotheridae	1	1	1	1	1			
Elephantidae								
Stegotetrabeladon			1	1				
Stegodibelon				1				
Primelephas			1	1				
Loxodonta				1	1	1	1	1
Elephas			1	1	1	1	1	
Mammuthus				1	1	1		
Mammutidae								
Zygolophodon				1				
Mammut	1							
Stegodon			1	1				
Deinotheridae								
Prodeinotherium	1	1	1					
Deinotherium			1	1	1			
Rhinocerotidae								
Brachypotherium	1	1	1	1				
Aceraterium	1	1						
Dicerorhinus	1							
Chilotheridium	1	1	1					
Paradiceros		1						
Diceros				1	1	1	1	1
Ceratotherium			1	1	1	1	1	1
Equidae								
Eurygnathohippus			1	1				
Equus				1	1	1	1	1
Hippopotamidae								
Hexaprotodon			1	1	1	1		
Hippopotamus				1	1	1	1	1
Suidae								
Notochoerus			1	1				
Kolpochoerus				1	1			
Metridiochoerus				1	1	1		
Giraffidae								
Palaeotragus	1	1	1					
Sivatherium			1	1	1	1		
Giraffa			1	1	1	1	1	1
Bovidae								
Taurotragus						1	1	1
Tragelaphus			1	1	1	1	1	1
Simatherium				1				
Syncerus					1	1	1	1
Pelorovis					1	1	1	
Megalotragus					1	1	1	
TOTAL	5	5	13	14	13	12	9	6

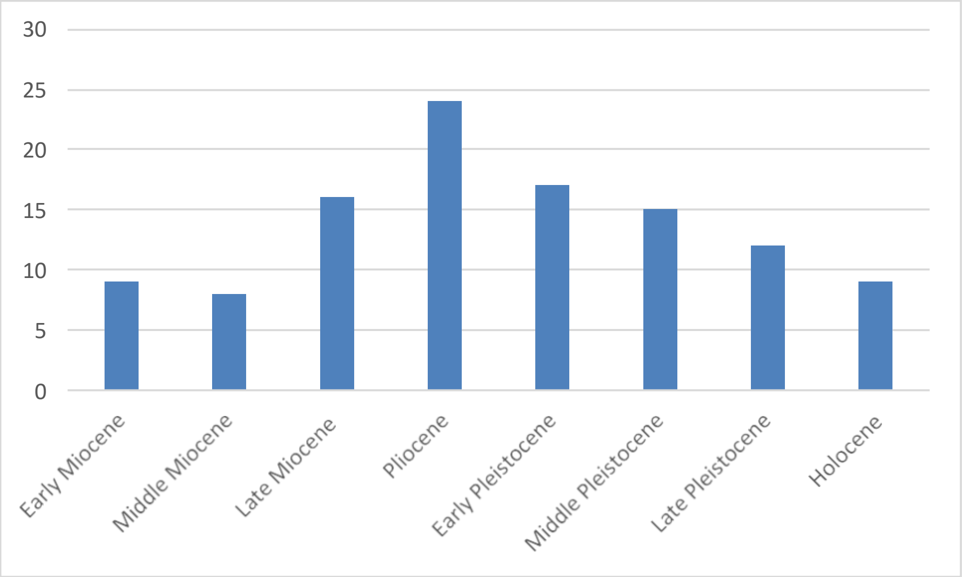


Figure 4.2. Graph showing numbers of large herbivorous mammal genera (>350 kg) living in Africa from the Miocene to the Holocene (information from Potts 1996 and Bobe 2006).

The aridification of Africa has been linked to the closing of the Indonesian Seaway, changes in current flow in the Indian Ocean (Cane and Molnar 2001; Bobe 2006), closure of the Isthmus of Panama, and changes in the Atlantic Ocean currents (Haug and Tiedemann 1998; Haug et al. 2001; Bobe 2006) (Figure 4.1). Animals that lived in woodland and forest habitats became concentrated in river valleys (Bobe 2006). For example, *Tragelaphus pricei* and *T. nakuae* were found in the Pliocene beds of the Omo Shungura Formation (Figure 3.3); *Tragelaphus* is the genus that contains kudus, nyalas and bushbuck, all of which are browsers. Other mammals, like the extinct gelada baboon *Theropithecus brumpti*, have been found in the Omo River and areas connecting it to the Turkana basin.

Global oscillations between arid and humid phases began just before the Plio-Pleistocene boundary (de Menocal 2004), with intervals of increased aridity at 2.8, 1.7 and 1.0 Ma (de Menocal 1995; Bobe 2006). The initial 2.8 Ma arid period, linked to bipolar glaciation, lasted approximately 41,000 years (de Menocal 2004). In response, Africa's climate became cooler, resulting in faunal and floral changes. The climatic cycles increased in duration with time, and after 1.0 Ma, the cool, dry periods lasted for around 100,000 years (de Menocal 2004). Several of Africa's living primate species, including humans, emerged during these 2 Ma of more fluctuating climatic and vegetation regimes.

CHAPTER FIVE: ASSEMBLING THE COMPARATIVE DATA

5.1. Extant non-human primate clades included in the analysis

For my study, I compared the phylogenies of five living primate clades (i.e., related species descended from a common ancestor) that occupy different habitats (e.g., forest, woodland, grassland) and have evolved in Africa over different time frames during the Cenozoic. I hypothesised that the evolution of these clades should reflect geological and palaeoclimatic events within different environments over the period covering the earliest emergence of a living lineage (late Eocene) to the Pleistocene.

5.1.1. Lorisoidea

The lorisoids have the deepest evolutionary origins of living African primates. Stem lorisoid fossils have been recovered from sediments 40 – 35 Ma old (see Tables 2.1 and 2.2, and section 2.2.1) and were apparently distributed from Egypt to Namibia. African lorisoids comprise two families: the fast-moving (vertical clinging and leaping) Galagidae, which includes the genera *Otolemur, Sciurocheirus, Galago, Euoticus*, *Galagoides* and *Paragalago* (Masters et al. 2017), and the slow-climbing Lorisidae, which includes the genera *Perodicticus* (pottos) and *Arctocebus* (angwantibos, or golden pottos) (Masters 2020). The galagids and lorisids diverged from one another in the late Eocene, between about 43 and 34 Ma (Figures 5.1, 5.2 and 5.3). Two genera of lorisids occur in South-east Asia, and shared a common ancestor with the African pottos during the Miocene. The fact that the oldest stem galagid fossils (*Saharagalago* and *Wadilemur*) are ~37 Ma (Seiffert et al. 2003) supports the older (43 Ma) estimate (Pozzi 2016).

All of the lorisoid primates are arboreal, and dependent on trees for locomotion and foraging. Hence, the eight African genera have evolved within the context of forest and woodland conditions that existed on the continent during the Cenozoic (Pozzi 2016). I compiled data regarding lineage divergence dates within the African lorisoids computed using molecular clock techniques, along with fossil and extant distribution data, in order to explore potential coincidences among evolutionary, tectonic and climatic events. Figures 5.1 and 5.2 show two comprehensive phylogenies of strepsirrhine (tooth-combed) primates (Springer et al. 2012; Herrera and Dávalos 2016, respectively), while Figure 5.3 represents the most recent phylogenetic analysis of the Galagidae (Masters et al. 2017, based on Pozzi 2016). These phylogenetic trees formed the basis of my reconstructed evolutionary scenarios within this superfamily. Although all three phylogenies included both nuclear and mitochondrial sequences, estimated divergence dates differ by more than 5 million years, depending on the sequences and analytical techniques used. Those of Springer et al. (2012) and Herrera and Dávalos (2016) were missing data for less accessible species. Hence, I regarded the dates reported by Pozzi (2016) as the most reliable and comprehensive (see Table 5.1).

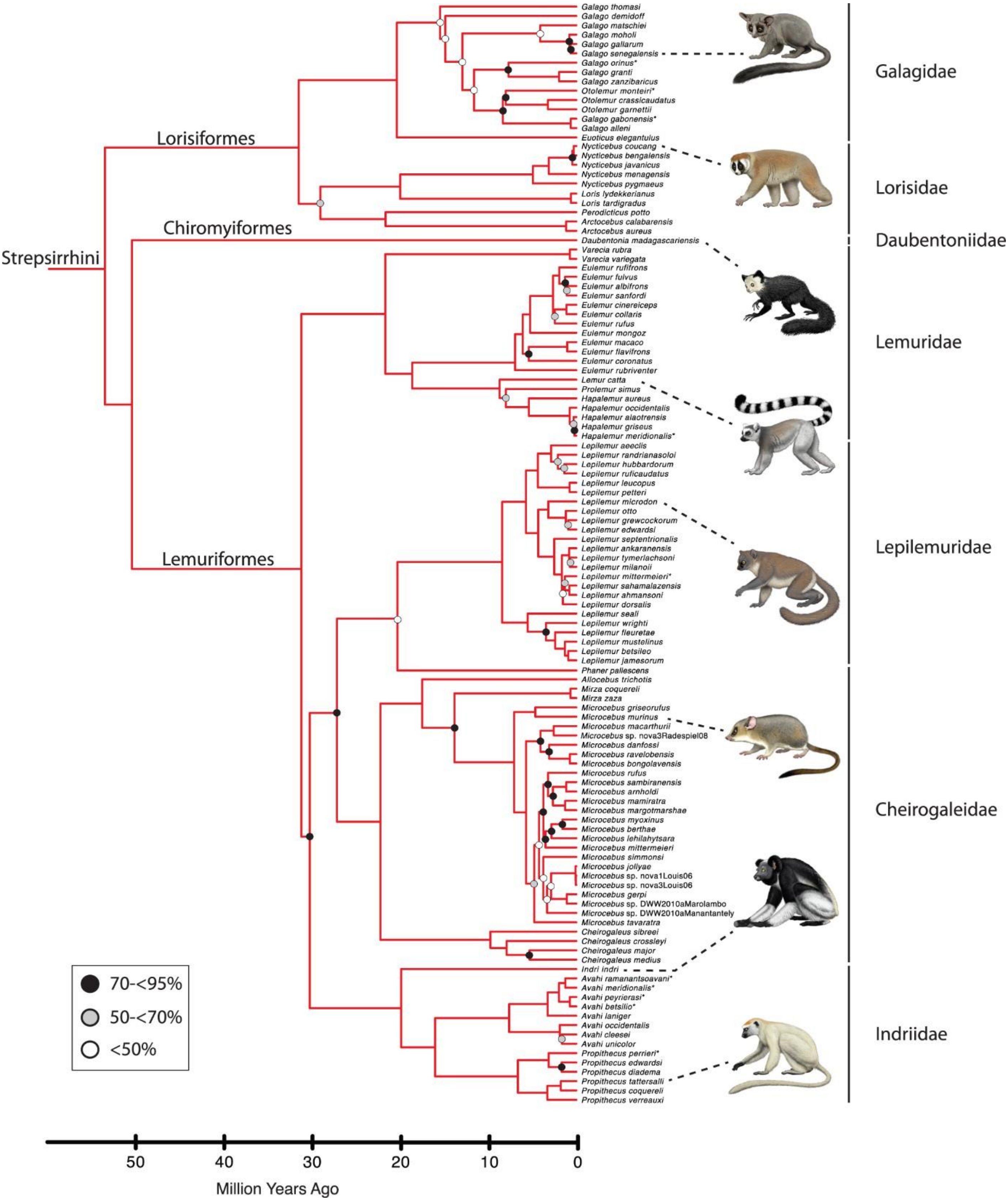


Figure 5.1. Phylogeny of the Strepsirrhini published by Springer et al. (2012) and based on both nuclear and mitochondrial DNA sequences.

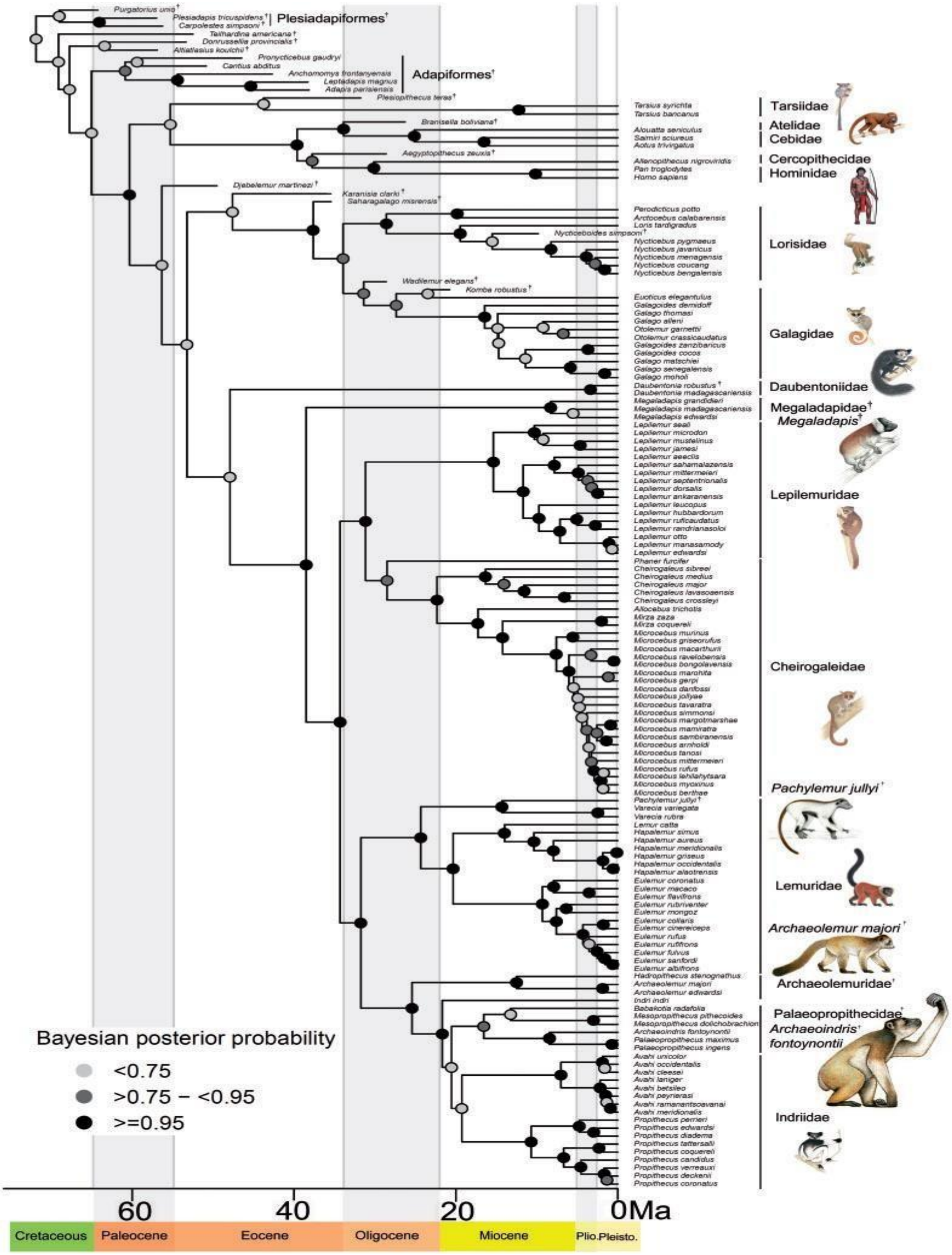


Figure 5.2. Phylogenetic reconstruction of extant and recently extinct strepsirrhine primates based on a combined morphological-molecular dataset (from Herrera and Dávalos 2016).

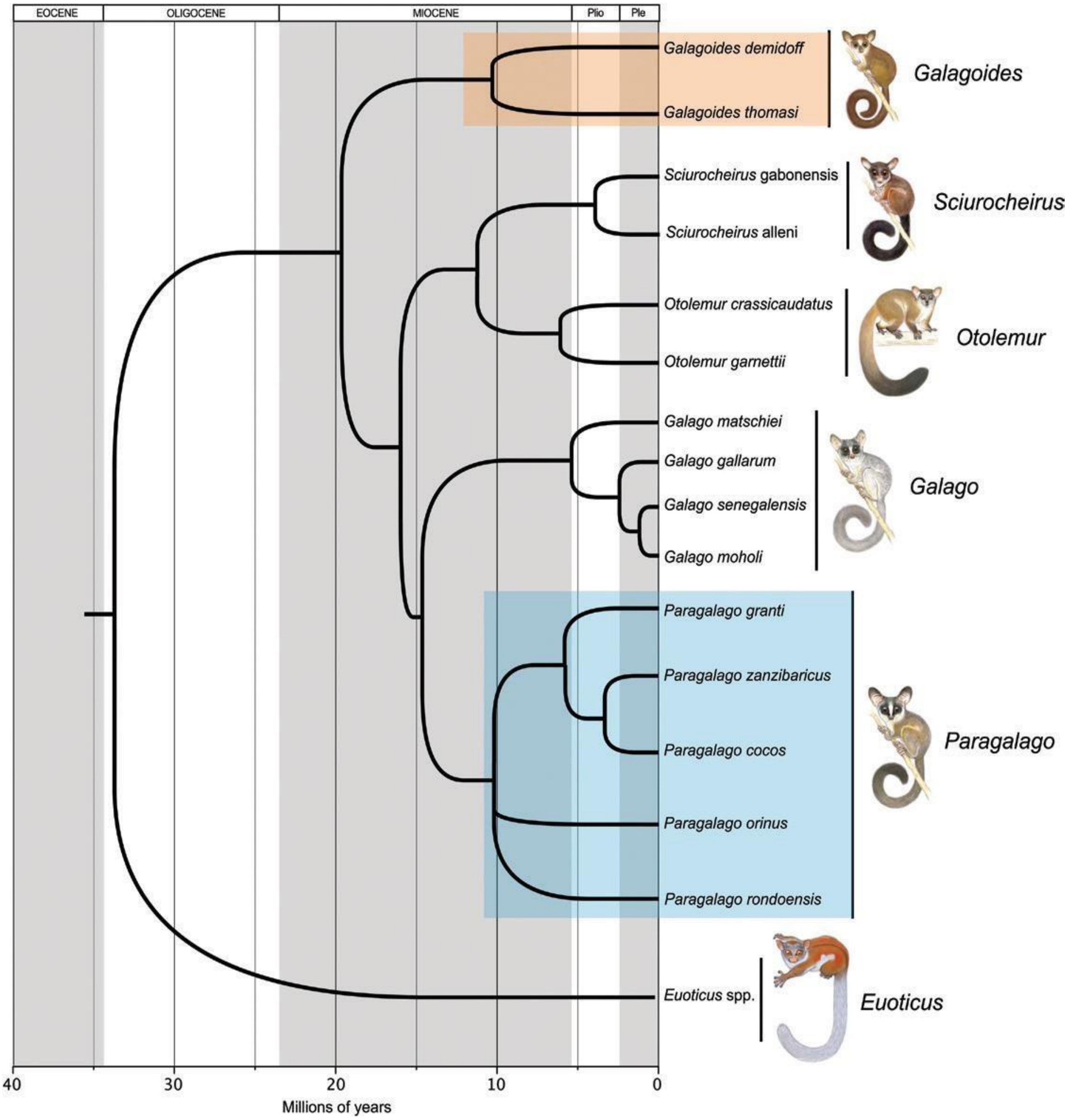


Figure 5.3. Most recent phylogenetic reconstruction of living Galagidae (from Masters et al. 2017, and based on the data of Pozzi 2016). The orange and blue rectangles indicate the polyphyletic origin of the two dwarf galago genera, previously classified within a single genus.

Table 5.1. Major divergence dates and locations among African lorisoid primates

Divergence event (Ma)	Springer et al. 2012	Herrera & Dávalos 2016	Pozzi 2016; Masters et al. 2017	Geographical area in Africa
Lorisidae-Galagidae	34.4	34	43	West-Central
Perodicticus – Arctocebus	22	20	-	West-Central
Euoticus	20	30	34	West-Central
Galagoides	17	16	20	West-Central
***Galagoides* spp.**	15	17	10	Central
Otolemur* + *Sciurocheirus	14	17	16	Central
Sciurocheirus	9	9	11	West
***Otolemur* spp.**	3.5	6	7	East
Paragalago – Galago	14	11	14.6	East
G. matschiei	5	8	5	Central
***Paragalago* spp.**	9 – 2.5	3	11 – 3.6	East
G. gallarum	1.5	-	2	East
G. moholi – G. senegalensis	1	1	1	East-Central

All galagids have elongated hind limbs and tarsal bones, although the tarsal regions of *Euoticus* (needle-clawed galagos) are the shortest of the clade, while those of the lesser galagos (*Galago*) are the most elongated (Masters and Bragg 2000). *Galago* species are capable of leaping distances up to 5 m between trees (McArdle 1981), which is probably an adaptation linked to their much more open habitats, including woodlands and isolated thickets.

The two potto genera, *Perodicticus* and *Arctocebus*, appear to have separated around the beginning of the Miocene epoch, 22 – 20 Ma (Springer et al. 2012; Herrera and Dàvalos 2016). Both genera occupy tropical forests, but *Arctocebus* is restricted to a small range in West-Central Africa, while *Perodicticus* is distributed from Guinea in the west to central Kenya in the east. Although there are only two extant genera of African lorisids, the family may have been more diverse in the past.

The extant Galagidae have a more extensive radiation, with six genera comprising 14 to 16 species (depending on the species concept applied). The four oldest genera, like the two potto genera, co-occur in the West-Central tropical forest, from eastern Nigeria through Cameroon to Congo and Gabon, making it highly likely that the African lorisoids originated in this region (DelPero et al. 2000; Pozzi 2016). The oldest extant genus is the shorter limbed *Euoticus* (needle-clawed galagos), which emerged around the Eocene – Oligocene boundary, 34 Ma (Pozzi 2016, Figure 5.3). This date coincides with a global mass extinction event, the Grande Coupure (Fleagle 2013), when the adapiform strepsirrhines largely went extinct.

The second lineage to emerge was *Galagoides*, the western dwarf galagos, which share the range of common pottos, from Guinea in the west to Rwanda and Uganda in the east, and also extend southwards into Angola (Svensson et al. 2017). The squirrel galagos, *Sciurocheirus*, which are largely sympatric with *Euoticus*, are the sister group of the East African greater galagos (DelPero et al. 2000), genus *Otolemur.* The *Otolemur – Sciurocheirus* clade diverged from the lesser galagos ~16 Ma; the two genera separated approximately 10 Ma, and the *Otolemur* species diverged in the late Miocene, 7-6 Ma (Pozzi 2016).

The two youngest genera, *Paragalago* and *Galago*, are medium- to small-sized galagos (60 – 250 g), which split from one another approximately 14 Ma and radiated into habitats outside of the West-Central African forest. *Paragalago* species are distributed east of the EARS, with one species (*P. orinus*) adapted to montane habitat, while the remaing four species are lowland taxa (Génin 2021). The genus *Galago* comprises four species, the oldest of which (*G. matschiei*) occurs in the tropical forest west of the EARS, in the eastern Democratic Republic of Congo and Rwanda, and diverged from its congeners 5 Ma, at the end of the Miocene, when Africa experienced dry conditions (Pozzi 2016). *Galago gallarum*, *G. moholi* and *G. senegalensis*, which occupy drier habitats, emerged during the Plio-Pleistocene, concomitant with the spread of wooded grassland habitats. The African lorisoid radiation thus reflects the emergence of different habitat types from the late Eocene to the Pleistocene, including rain forests, montane forests, woodlands and bushveld.

5.1.2. Hominoidea

Superfamily Hominoidea includes the lesser apes (Hylobatidae) and great apes (Hominidae) (Figure 5.4).

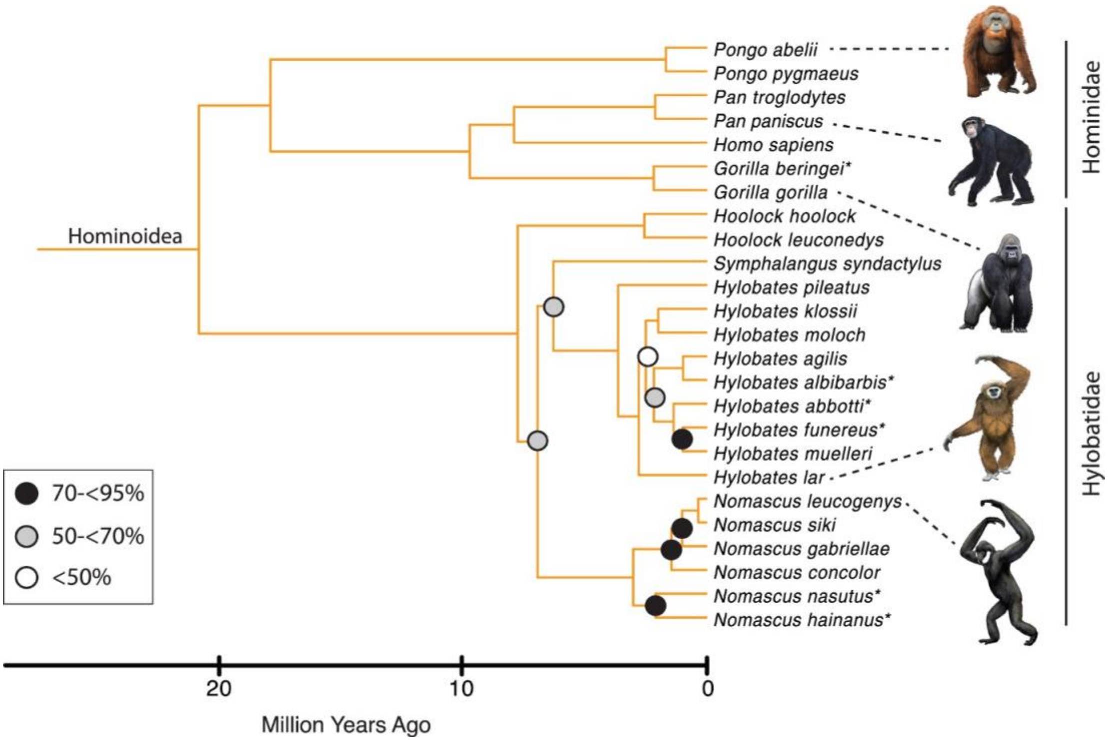


Figure 5.4. Phylogenetic relationships among the living apes (Superfamily Hominoidea) as reconstructed by Springer et al. (2012). The black circles show nodes with high credibility, while the grey and white circles depict nodes with little support.

The family Hylobatidae comprises three genera and at least 15 species, although the deeper divergences among the gibbons are not well resolved, which may imply that some of the recognised species do not represent independent lineages. All of the nodes separating the great ape genera, *Pongo*, *Gorilla*, *Pan* and *Homo*, were strongly supported. Each of the two African great ape genera (*Gorilla* and *Pan*) have two extant species, while *Homo* has one surviving species. Divergence dates according to Springer et al. (2012) are summarised in Table 5.2.

Table 5.2. Family and generic divergence dates and locations among African and Asian apes

Divergence event (Ma)	Springer et al. 2012	Geographical area
Hominidae-Hylobatidae	21	South-east Asia
Gorilla* – *Pan* + *Homo	10	West-Central Africa
Pan* – *Homo	8	Central Africa
***Pan* spp.**	2	West-Central Africa

Although apes were present in Africa throughout the Miocene, and fossil representatives of Family Hominidae were present at least 14 Ma in East Africa (see *Kenyapithecus* in Table 2.2), the divergence between the living great and lesser apes clearly occurred in Asia. Gorillas (*Gorilla* spp.), the oldest divergence among living African apes, are restricted to the west of the EARS, as are the chimpanzee (*Pan*) species. It is hence possible that the *Homo* – *Pan* split occurred in the central African region, possibly in connection with uplift of the western branch of the rift system.

5.1.3. Cercopithecoidea

According to molecular estimates, the two tribes of the Cercopithecinae (cheek pouch monkeys), the Cercopithecini (guenons) and Papionini (baboons and mangabeys), separated between 15 and 11 Ma (Lo Bianco et al. 2017). Hence, the radiation of the cercopithecines and the African apes took place almost 20 Ma later than that of the lorisoids. Nevertheless, many of the taxa in these different clades overlap in their habitat requirements, and have shared sympatric distributions since the middle Miocene. As a result, the diversification of their lineages was influenced by the same geotectonic and palaeoclimatic events. A comparison of generic and specific divergence dates among them was therefore undertaken.

A comprehensive phylogeny of the cercopithecoids based on both mtDNA and nDNA was reconstructed by Springer et al. (2012), and is shown in Figure 5.5.

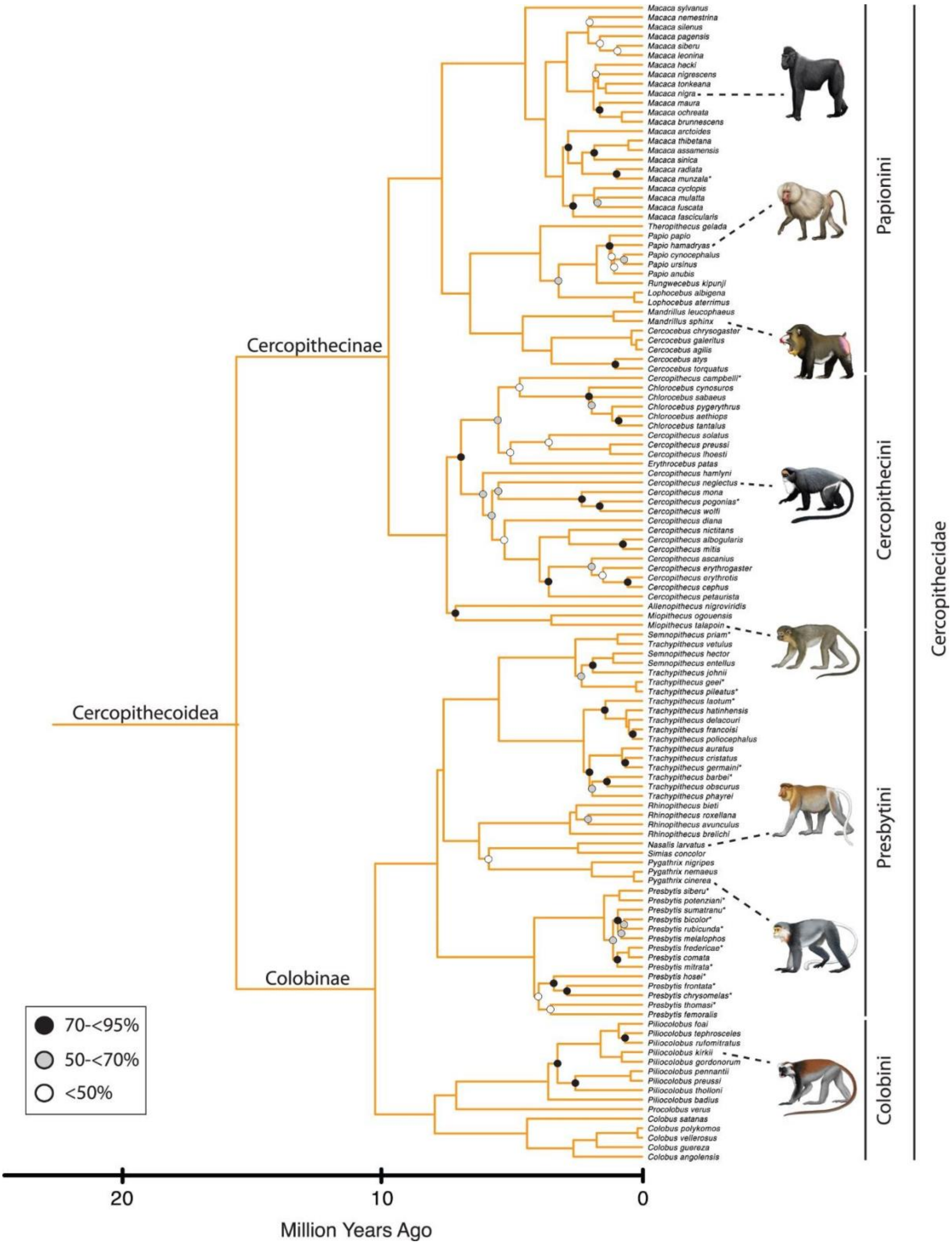


Figure 5.5. Phylogenetic tree describing the evolution of the family Cercopithecidae, based on a supertree compiled from both mitochondrial and nuclear DNA sequences (from Springer et al. 2012). Note that many divergence dates occur between 7 and 5 Ma.

5.1.3.1. Guenons

The tribe Cercopithecini is the most diverse clade of Old World monkeys (Catarrhini), including six genera (*Allenopithecus*, *Allochrocebus*, *Cercopithecus*, *Chlorocebus*, *Erythrocebus* and *Miopithecus*) with 34 species. Most of these species fall under the genus *Cercopithecus*, and are largely arboreal. *Allenopithecus* (swamp monkeys) and *Miopithecus* (talapoins) are relatively ancient, and diverged early in the cercopithecin radiation (Figure 5.5). Three semi-terrestrial genera, *Chlorocebus* (vervet monkeys), *Allochrocebus* (mountain monkeys), and *Erythrocebus* (patas monkeys), have been separated from *Cercopithecus* because they compromise the monophyly of the genus in some reconstructions (Lo Bianco et al. 2017).

The ~20 *Cercopithecus* species have been grouped into seven superspecies (species groups). For ease of analysis, I focussed on the hypothesised relationships among these groups rather than those of all of the component species, to clarify the different evolutionary scenarios implied by the different phylogenetic trees. The species groups recognised include: the ***C. cephus*** group (including *C. ascanius*, *C. cephus*, *C. erythrogaster*, *C. erythrotis* and *C. sclateri*), the ***C. diana*** group (*C. diana* and *C. roloway*), the ***C. hamlyni*** group *(C. hamlyni* and *C. lomamiensis*), the ***C. mona*** group (*C. campbelli*, *C. denti*, *C. lowei*, *C. mona*, *C. pogonias* and *C. wolfi*), ***C. neglectus*** and the ***C. nictitans*** group (*C. albogularis*, *C. doggeti*, *C. kandti* and *C. mitis*). *Cercopithecus dryas* is also a distinct group.

Within *Cercopithecus*, hybridisation is not uncommon, even among species with very different karyotypes, and some newly recognised species may in fact be hybrids (e.g., the dryad monkey, *C. dryas*; Lo Bianco et al. 2017). Because mitochondrial DNA is largely maternally inherited, phylogenies based on mtDNA and nDNA are likely to yield different tree topologies. Phylogenies reconstructed from nDNA sequences (e.g., Perelman et al. 2011; Springer et al. 2012) indicate that the semi-terrestrial genera (*Allochrocebus*, *Chlorocebus* and *Erythrocebus*) are closely related, and that terrestrial adaptations evolved in a common ancestor (Figures 5.5. and 5.6). The most comprehensive phylogeny reconstructed from mtDNA (Guschanski et al. 2013) does not recover this clade (Figure 5.5). Inconsistent tree topologies, even among reconstructions based on similar kinds of data, have complicated our understanding of guenon evolution. For example, Springer et al. (2012) grouped the ancient West African genera *Allenopithecus* and *Miopithecus* as sister taxa (Figure 5.5), whereas Perelman et al. (2011) assigned *Allenopithecus* to the base of the semi-terrestrial clade, and *Miopithecus* as sister to the arboreal clade (Figure 5.6). The mtDNA tree presented them as independent outgroups to the rest of the guenon radiation (Figure 5.6).

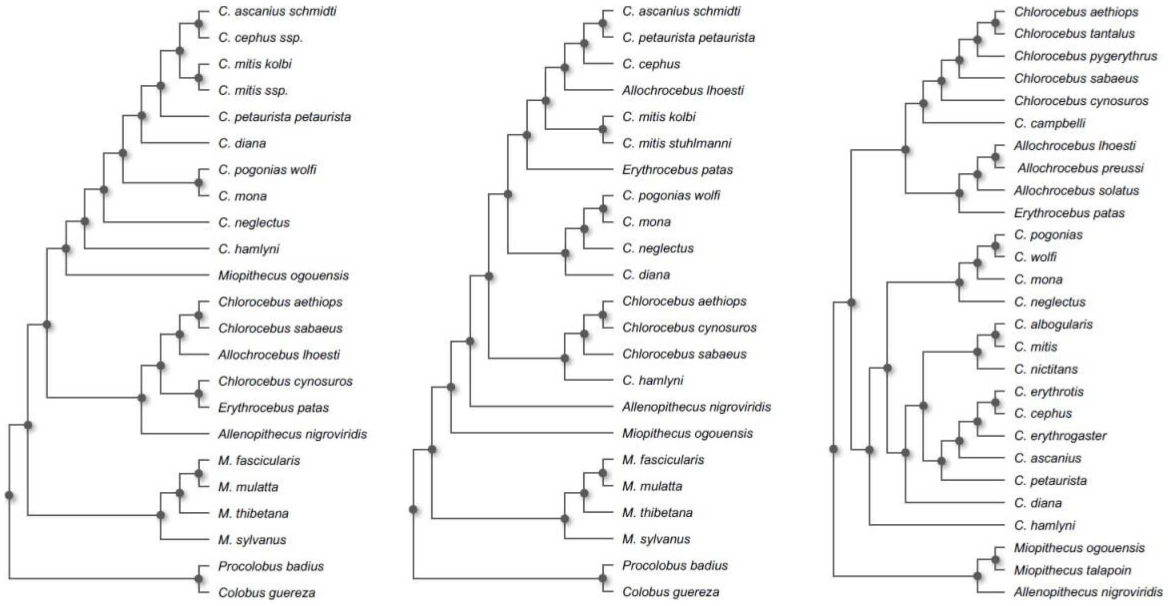


Figure 5.6. Phylogenies of Cercopithecini based on nuclear DNA (left, data from Perelman et al. 2011), mitochondrial DNA (middle, data from Guschanski et al. 2013), and nuclear + mitochondrial DNA (right, data from Springer et al. 2012) (from Lo Bianco et al. 2017).

Tables 5.3 and 5.4 present lineage divergence dates based on nDNA and mtDNA, repectively, along with their most likely area of origin.

Table 5.3. Divergence dates of Cercopithecini based on nDNA in Ma.

Divergence event	Springer et al. 2012	Perelman et al. 2011	Geographical area in Africa
Cercopithecini – Papionini	10	11.5	West-Central
Allenopithecus* + *Miopithecus	7.8	8.2	West-Central
Semi-terrestrial – arboreal clades	7.2	7.6	West-Central
***C. hamlyni* – arboreal clade**	6.0	6.2	West-Central
C. neglectus* + *C. mona* – *C. diana* + *C. cephus* + *C. nictitans	5.4	6.0	West Africa
Allochrocebus* + *Erythrocebus* – *Chlorocebus	5.5	5.0	West Africa
C. diana* – *C. cephus* + *C. nictitans	5.0	5.2	West-Central
Allochrocebus* - *Erythrocebus	5.0	4.5	West Africa
***C. cephus* speciation**	3.6	3.5	West Africa
C. cephus* – *C. nictitans	4.0	2.9	West Africa
***Chlorocebus* speciation**	2.2	1.5	West-Central

Table 5.4. Divergence dates of Cercopithecini based on mtDNA in Ma.

Divergence event	Guschanski et al. 2013	Geographical area in Africa
Cercopithecini-Papionini	12.3	West-Central
Miopithecus	9.6	West-Central
Allenopithecus	9.3	West-Central
C. hamlyni* + *Chlorocebus* + *C. dryas	7.5	West-Central
C. diana* + *C. mona* + *C. neglectus	7.4	West Africa
Erythrocebus* – *Allochrocebus* + *C. cephus* + *C. nictitans	7.1	West Africa
C. diana* – *C. mona* + *C. neglectus	6.2	West Africa
C. nictitans* – *Allochrocebus* + *C. cephus	5.8	West Africa
C. mona* – *C. neglectus	5.5	West Africa
C. mona* + *C. campbelli* – *C. pogonias	3.0	West Africa
Allochrocebus* – *C. cephus	3.0	West-Central
C. mitis* – *C. nictitans	2.4	West-Central
***C. nictitans/mitis* speciation**	2.4 – 0.5	West-Central/East
***C. cephus* speciation**	2.45	West Africa
***Chlorocebus* speciation**	2.45 – 1.0	West-Central
C. hamlyni* – *Chlorocebus	2.3	West-Central
***C. poginias* speciation**	2.2	West-Central

Nuclear DNA indicates that the radiation of the guenon monkeys began with the divergence of the two ancient taxa: *Allenopithecus*, swamp monkeys of the West-Central Congo; and *Miopithecus*, talapoins from the coastal rain forest areas extending from southern Cameroon to northern Angola. Both of these genera show pleisomorphic features shared with papionins: male swamp monkeys have fused ischial callosities, and female talapoins have sexual swellings (Butynski et al. 2013). Nuclear DNA estimates these divergences around 8 Ma, which is broadly coeval with the time of spread of C_4 grasslands in Africa (section 4.2.3). In contrast mtDNA places these changes a million years earlier, around 9 Ma. The more rapid substitution rates in mtDNA often yield slightly greater ages. Nuclear data place the divergence between the semi-terrestrial and arboreal cercopithecin taxa shortly after, around 7.5 Ma, while mtDNA does not recover such a clade. These dates coincide with the late Miocene aridification of Africa, which would have isolated animals dependent on rain forests and possibly favoured the evolution of semi-terrestrial characteristics and behaviours in the common ancestor of *Allochrocebus*, *Chlorocebus* and *Erythrocebus*. The semi-terrestrial genera began to diverge from one another 5 Ma, which coincides with the peak of aridity during the Messinian crisis. If the mtDNA date is more accurate, these traits would have evolved independently much later: 7 Ma for *Erythrocebus*, 3 Ma for *Allochrocebus* (diverging from the arboreal *C. cephus*), and 2.3 Ma for *Chlorocebus* (diverging from the arboreal *C. hamlyni*). The scenario supported by nDNA is more parsimonious, as described above.

The first divergence among the arboreal *Cercopithecus* monkeys was the *C. hamlyni* group (owl-faced monkeys). Mitochondrial DNA estimates this split at ~7.5 Ma, while nDNA proposes a date around 6 Ma. The remaining arboreal species groups either diverged between 6 and 5 Ma (nDNA) or between 7 and 6 Ma (mtDNA), but the tree topologies (phylogenetic relationships) are vastly different for the two data sources. LoBianco et al. (2017) posited that the late Miocene aridification would have fragmented the tropical and subtropical forests and the monkey populations that depended on them, leading to allopatric divergence and speciation. Speciation within these separated lineages was evidently linked to the climatic oscillations and changes in regional landscapes that occurred during the Plio-Pleistocene epoch. The dates estimated for these terminal divergences tend to be slightly older for nDNA than mtDNA. Speciation within the *C. cephus* group took place 3.6 – 2.45 Ma; the *C. pogonias* group radiated around 2.2 Ma; and the *Chlorocebus* diversification occurred between 2.45 and 1 Ma (Tables 5.3 and 5.4).

West, Central and East Africa’s vegetation during the middle Miocene (~14 Ma) appears to have consisted largely of forests and woodlands. Around 12.5 Ma (see section 4.2.3), a significant period of cooling and drying was initiated, reaching a peak at 5 Ma, in response to glaciation (Lo Bianco et al. 2017). These climatic changes contributed to much more heterogenous environments made up of forests, dry woodland and savanna grasslands, which may have been ideal conditions for driving diversification among the Cercopithecinae, first in terms of the split between the largely terrestrial papionins and the arboreal cercopithecins, and then by the radiation of the guenon lineages.

5.1.3.2. *Chlorocebus* (vervet or savanna monkeys)

Vervet monkeys are found across sub-Saharan Africa and have diversified within the last 2 Ma (Perelman et al. 2011; Springer et al. 2012; Guschanski et al. 2013). Their preferred habitat includes woodland savanna and gallery forests, which are relatively recently derived environments. Vervet monkeys are often seen on the ground foraging or crossing open spaces, although they move equally easily in trees; terrestrial locomotion makes up only 20% of their activity (Fleagle 2013), while the remainder is arboreal. Their diet consists of fruits, gums, shoots and invertebrates. A population of vervets from Senegal (*C. sabaeus*) hunts crabs like the crab-eating macaques of South-east Asia (Fleagle 2013). Six largely allopatric taxa have been recognised (see Figure 5.7).

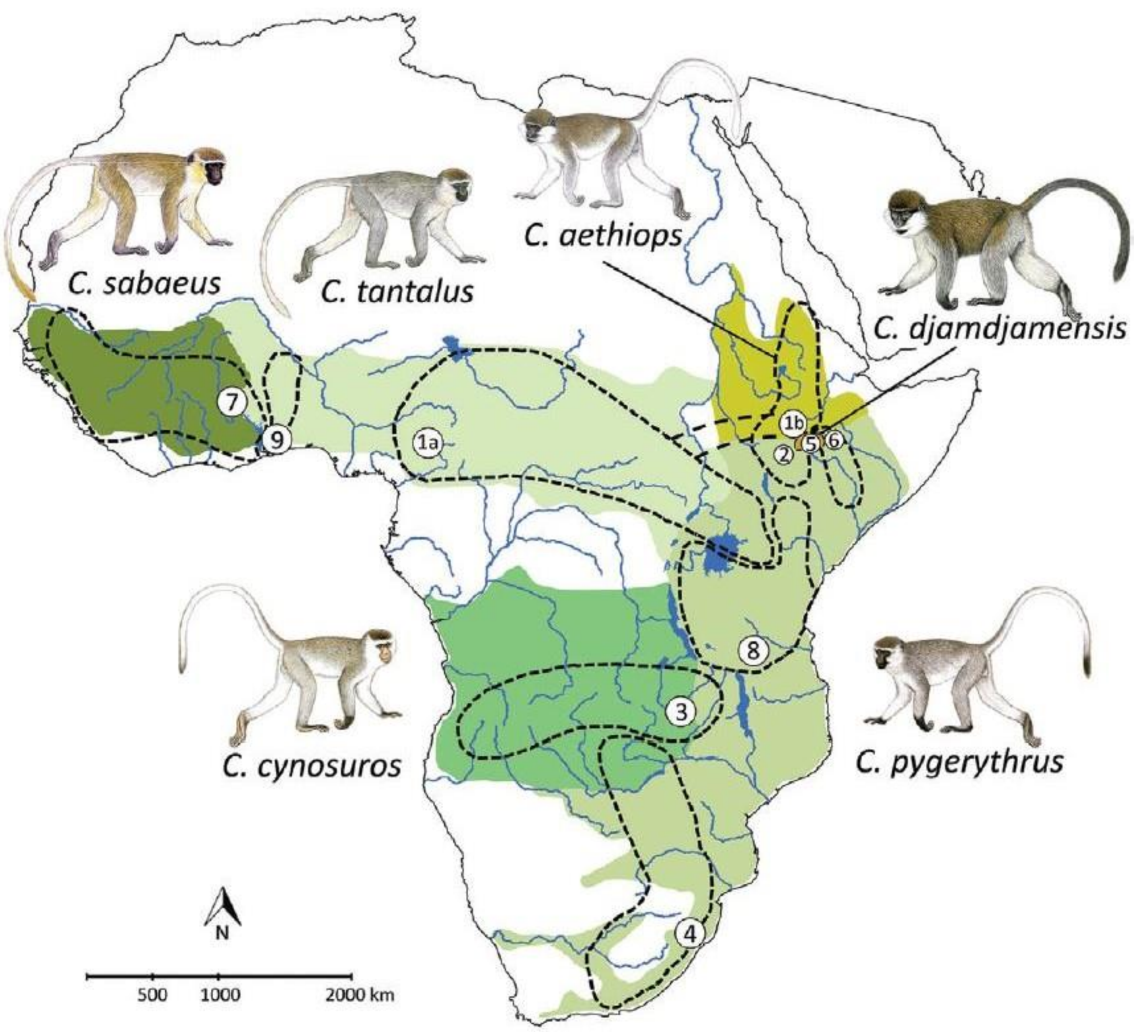


Figure 5.7. Geographic and taxonomic diversity of the genus *Chlorocebus* (from Dolotovskaya et al. 2017). The majority of species diversified within the EARS.

In all reconstructions, the oldest lineage to diverge from the rest of the clade is *C. sabaeus*, the green monkey (Figure 5.8), which has the most westerly modern distribution and is endemic to the savannas of Guinea and the Sahel, as well as the rain forest-savanna mosaic west of the Volta River. This divergence must therefore have occurred between West and East-Central Africa.

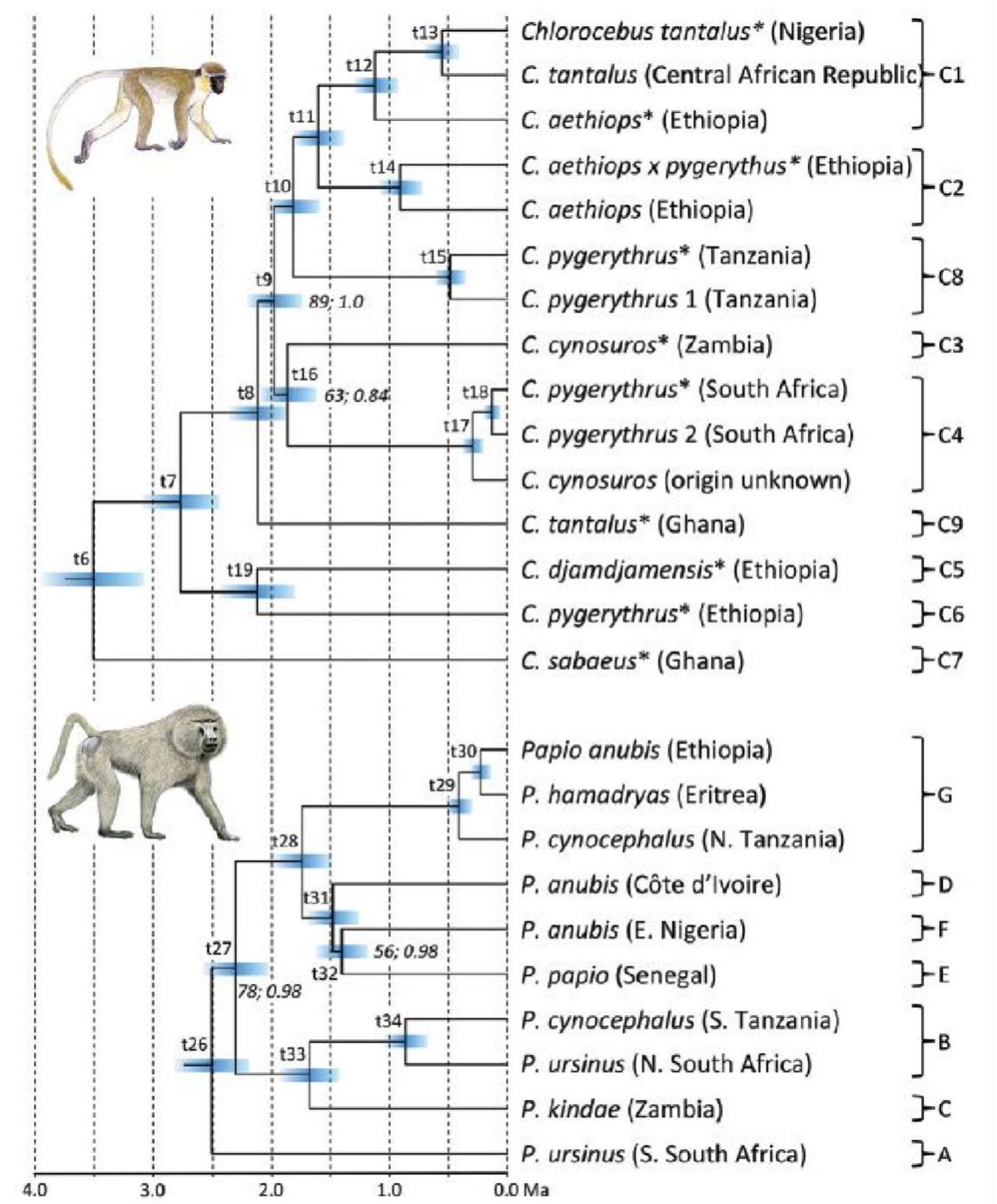


Figure 5.8. Comparative phylogenies of vervet monkeys (*Chlorocebus* spp.) and baboons (*Papio* spp.) reconstructed by Dolotovskaya et al. (2017). C1 – C9 indicate the nine putative mtDNA clades of savana monkeys, and A – G indicate the 7 putative mtDNA clades of baboons. All nodes are numbered (*Chlorocebus*: t6-t18; *Papio*: t26-t34). Nodes t9, t16, t27 and t32 have bootstrap values lower than 100% and prior probablities lower than 1.0; the rest of the nodes are fully supported. The blue bars represent 95% confidence intervals of divergence times. Note that most of the divergence dates within clades fall between 2.5 and 1.5 Ma.

However, whether these taxa constitute true species is a matter of debate. The phylogeny in Figure 5.8 shows a great deal of paraphyly and even polyphyly, and several mtDNA phenotypes are found in more than one clade, which probably indicates a substantial amount of interbreeding between lineages. The only taxa that appear monomorphic are *C. sabaeus* and *C. djamdjamensis*, which is unsurprising as each lineage is represented by a single specimen. The mtDNA phenotypes therefore represent geographically separated populations, not nominate species (Dlotovskaya et al. 2017), and are better considered as subspecies.

The problem of introgression of complete mitochondrial haplotypes in hybridisation events is demonstrated by a manifest difference in topology between mtDNA trees based on samples taken from different geographic populations (Warren et al. 2015; Dolotovskaya et al. 2017). Moreover, divergence dates vary considerably based on different methods of calibrating the molecular clock. Warren et al. (2015) estimated lineage divergence dates using calculated substitution rates, and their summary, which lacked *C. a. djamdjamensis*, is detailed in Table 5.5.

Table 5.5. Divergence dates of *Chlorocebus* subspecies based on mtDNA (Warren et al. 2015) in ka.

Divergence event	ka	Geographical area in Africa
C.a. sabaeus* – other *Chlorocebus	531	West – East split
C. a. aethiops – C. a. tantalus + C. a. cynosuros + C. a. pygerythrus	446	North-East – Central split
C. tantalus – C. a. cynosures + C. a. pygerythrus	265	Central – South-East split
C. a. cynosuros – C. a. pygerythrus	129	South-West – South-East split

In contrast with the speciation of the arboreal geunons, Warren et al. estimated all genetic divergences within *Chlorocebus* to be middle to late Pleistocene in age, starting with the divergence of *C. a. sabaeus* at 531 ka, *C. a. aethiops* at 446 ka, *C.a. tantalus* at 265 ka, and the final separation between *C.a. cynosuros* and *C.a. pygerythrus* at 129 ka. The oldest separation thus occurred just south of the Sahara, while the more recent fragmentation occurred in the southern African region, showing a north-south migration.

A second study by Dolotovskaya et al. (2017) was based on complete mitochondrial genomes comprising > 16,000 base pairs, and including all 6 recognised taxa. In addition, their molecular clock estimates were calibrated using the fossil record. Consequently, they produced a different tree with vastly different divergence dates (Figure 5.8; Table 5.6). In their analysis, the *Chlorocebus* radiation occurred in the late Pliocene to early Pleistocene.

Table 5.6. Divergence dates of *Chlorocebus* subspecies based on complete mtDNA genomes (Dolotovskaya et al. 2017) in Ma

Divergence event	**Ma**	**Geographical area in Africa**
C.a. sabaeus* – other *Chlorocebus	3.5	West – East split
***C. a. aethiops* + *C. a. cynosuros* + *C. a. tantalus* + *C. a. pygerythrus* (south) – *C. a. djamdjamensis* + *C. a. pygerythrus* (north)**	2.8	Northeast
***C. a. djamdjamensis* – *C. a. pygerythrus* (north)**	2.1	Northeast
***C. tantalus* – *C. a. aethiops* + *C. a. cynosuros* + *C. a. pygerythrus* (south)**	2.1	Central – Southern split
***C. a. cynosuros* – *C. a. pygerythrus* (south)**	2.0	South-Central – Southeast split
C. a. aethiops	1.65	Northeast

As before, *C. a. sabaeus* was the first lineage to diverge from the rest of the clade, an event dated at 3.5 Ma. The second major divergence was a clade comprising two taxa from Ethiopia, *C. a. djamdjamensis* (the Bale monkey) and *C. a. pygerythrus*, at 2.8 Ma. The northern *C. a. pygerythrus* individuals did not group with conspecifics from South Africa, which clustered with *C. a. cynosuros*, the malbrouk from South-Central Africa. The third potential divergence was *C. a. tantalus* from Central-West Africa, but this taxon was not monophyletic. Southern *C. a. pygerythrus* and *C. a cynosuros* diverged around 2 Ma, probably in South-Central Africa. I have included information from both studies in my final analysis to compare with locations of known geomorphic events during the Cenozoic.

5.1.3.3 Baboons

The papionins are medium to large sized monkeys that include the macaques (*Macaca*), the mangabeys of central Africa (*Lophocebus*, *Cercocebus*), the forest drills and mandrills (*Mandrillus*), the kipunji or highland mangabey of Tanzania (*Rungwecebus*), and the baboons (*Theropithecus, Papio*). Mangabeys were once classified within a single monophyletic group, but molecular genetics revealed that the similarities between *Lophocebus* and *Cercocebus* species were acquired convergently after the genera evolved from different ancestors (Disotell 1996). *Cercocebus* species are referred to as drill mangabeys because of their close relationship to the genus *Mandrillus*. They are large, semi-terrestrial animals indigenous to the humid forests of equatorial Africa. *Lophocebus* species are more closely related to baboons (baboon mangabeys). The kipunji, *Rungwecebus*, was previously classified under *Lophocebus*, but its genetic distinction led to it being given its own genus. Molecular evidence shows that the *Mandrillus-Cercocebus* (closed habitat papionins) and *Papio-Lophocebus-Theropithecus* (open habitat papionins) split occurred around 7 Ma (Springer et al. 2012; Figure 5.5), during the late Miocene.

Living baboons comprise two genera: *Papio*, distributed throughout sub-Saharan Africa, and *Theropithecus*, or gelada baboons, endemic to the Central Ethiopian plateau. *Theropithecus gelada* is the only living member of its genus, although gelada fossils have been found throughout Africa (section 2.2.4 and Table 2.5). The genus *Papio* diversified after the spread of grasslands at the end of the Miocene, and is largely terrestrial, although baboons often rest and feed in trees. Five *Papio* species have long been recognised (Figure 5.9), which range over most of sub-Saharan Africa and Arabia: *P. anubis, P. cynocephalus, P. hamadryas, P. papio* and *P. ursinus*. A sixth taxon, *P. kindae*, derives 52% of its genome from *P. ursinus*, and 48% from an unkown northern species, probably extinct (Rogers et al. 2019).

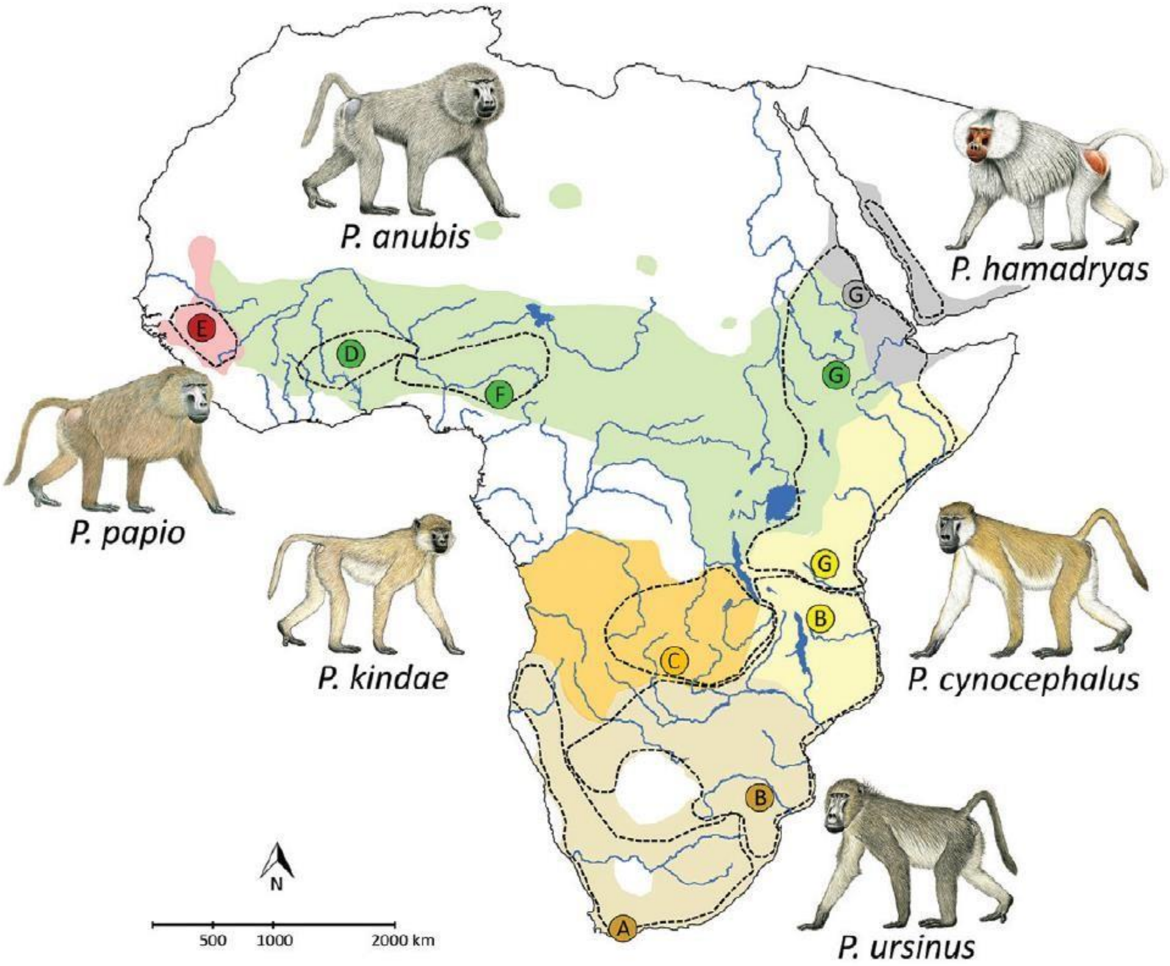


Figure 5.9. Geographic and taxonomic diversity of the genus *Papio* (from Dolotovskaya et al. 2017). While the boundary between *P. kindae* and southern *P. cynocephalus* coincide with tectonic structures of the EARS, the ranges of the northern taxa are less reflective of rifting, and possibly more related to uplift of the Ethiopian highlands.

Like the *Chlorocebus* radiation, the diversification of *Papio* is relatively recent (2 Ma), resulting in the same quandary as that presented by recently emerged cercopithecin species: (a) recently derived populations hybdridise relatively frequently; (b) morphotypes and genotypes do not always coincide; (c) nDNA yields different phylogenies from mtDNA; and (d) mtDNA phenotypes may differ between local conspecific populations. As a result, mitochondrial phenotypes often show paraphyly and even polyphyly, as in the savanna monkeys (Zinner et al. 2013; Boissinot et al. 2014). Unlike vervets, however, the six baboon lineages are clearly distinguishable both morphologically and behaviourally, and have maintained this distinctiveness despite gene introgression. They are therefore accorded full species status. The coincidence between the timing and geography of their radiation and that of *Homo* has led to them being considered good models for human evolution (Strum and Mitchell 1987; Rogers et al. 2019).

In the reconstruction of Springer et al. (2012) (see Figure 5.5), the cercopithecin and papionin primates diverged approximately 10 Ma, while the genus *Papio* diverged from its sister group *Theropithecus* 3.75 Ma. The cercopithecin – papionin split is likely to have occurred in West Central Africa (Table 5.3). The radiation within *Papio* appears to have occurred entirely within the Pleistocene (Table 5.7), and to have been initiated by the divergence of *P. ursinus* in the south. In the reconstruction of Zinner et al. (2013), the remaining clade, which included both southern and northern taxa, split again 2.3 Ma, separating *P. cynocephalus-P. ursinus* and *P. kindae* from the northern taxa, *P. anubis, P. hamadryas* and *P. papio* (Figure 5.8). The eastern *P. anubis – P. hamadryas* clade, which still undergoes periodic hybridisation, separated from the western *P. papio – P. anubis* clade 1.75 Ma, with *P. anubis* and *P. papio* separating 1.45 Ma. The yellow and chacma baboons, *P. cynocephalus* and *P. ursinus*, appear to have diverged between 0.9 and 1.5 Ma, while *P. anubis* and *P. hamadryas* speciated in northeastern Africa, possibly as recently as 250 ka, although their continuing hybridisation may have eroded the original split information.

Table 5.7. Divergence dates (Ma) of *Papio* lineages based on mitochondrial (Zinner et al. 2013) and nuclear (Boissinot et al. 2014) data

Divergence event	Zinner et al. 2013	Boissinot et al. 2014	Geographical area in Africa
Papio ursinus* – other *Papio	2.5	1.3 – 1.5	South
North – South split	2.3	0.9 – 1.2	East-Central
West – East split	1.75	0.5 – 0.9	Central
P. kindae – P. cynocephalus + P. ursinus	1.7	-	South-Central
P. anubis – P. papio	1.45	-	West
P. cynocephalus – P. ursinus	0.9	1.3 – 1.5	East-Central
P. anubis – P. hamadryas	0.25	-	Northeast

The biogeographic pattern of radiation among baboons is therefore very different from that of the savanna monkeys, despite the fact that the two clades have similar habitat requirements and diversified over similar time frames. *Chlorocebus* monkeys appear to have diverged from their closest living relatives in West Africa, and migrated east and then south within Africa. Baboons apparently originated in the south around 2.5 Ma, but were prevented from migrating north because of the tropical rain forest barrier (Zinner et al. 2013; Boissinot et al. 2014; Dolotovskaya et al. 2017). The split between northern and southern clades occurred slightly later, 2.3 Ma. The northern populations then spread from the west coast of West Africa across the continent to the east coast, where the most recent divergence occurred 0.25 Ma. Most authors (Zinner et al. 2013; Boissinot et al. 2014; Dolotovskaya et al. 2017) attribute the radiation of the baboons to repeated periods of population fragmentation and recontact in response to alternating cold and dry phases interspersed with hot and humid phases. Boissinot et al. (2014) proposed that corridors linking savanna areas would probably have been closed during humid periods, so that the different baboon morphotypes evolved by vicariance, in allopatry. The subsequent opening of these corridors during dry periods would have allowed the populations to expand and possibly encounter one another, leading to hybridisation. The increased erosion and changing river systems may have also influenced their different environments.

5.2 Methods of analysis

5.2.1. Combined assessment of primate lineage divergence dates

To understand how major lineage divergence dates estimated for the five primate clades studied here relate to one another, I combined the data presented in Tables 5.1 to 5.7 into a single chronological table (Table 5.8). I included both minimum and maximum dates, where possible. I then estimated the geographical areas in Africa where the divergences between major lineages are likely to have taken place, based on current distributions.

As mentioned above, reconstructing phylogenies using DNA sequences among the Cercopithecoidea (i.e., the guenons and baboons) is complicated by two factors: first, many of the splits are relatively recent, and nDNA sequences may not have accumulated enough mutations to provide a robust database. On the other hand, mtDNA, which accumulates substitutions at a much higher rate, is compromised by the relatively frequent hybridisation events that have occurred both between cercopithecin species and between papionin species. Because nDNA and mtDNA may yield very different tree topologies, possibly because of hybridisation, I relied primarily on the nDNA topologies and divergence dates for the older nodes, or when the two data sources yielded different trees. I included mtDNA information to increase the age estimates when appropriate, as well as in the case of recent speciation events.

Figure 5.10 is a map of the broad areas in Africa where I estimated that the non-human primate clades originated according to their current distributions. They are colour-coded in accordance with the regions in Table 5.8.

Table 5.8. Divergence dates (Ma) and likely geographical origins of African primate lineages. Epochs are shaded from violet to pink. Distributions are shaded from emerald green (west) to yellow (east).

Divergence event	Minimum	Maximum	Geographical area in Africa
Lorisidae-Galagidae	34	43	West-Central
Hominidae-Hylobatidae	21	21	(SE Asia)
Perodicticus – Arctocebus	20	22	West-Central
Euoticus	20	34	West-Central
Galagoides	16	20	West-Central
Otolemur + Sciurocheirus	14	17	Central
Paragalago – Galago	11	14.6	East
***Galagoides* spp.**	10	17	Central
Cercopithecini – Papionini	10	11.5	West-Central
Gorilla – Pan + Homo	10	10	West-Central
Sciurocheirus	9	11	West-Central
Pan – Homo	8	8	Central
Allenopithecus + Miopithecus	7.8	9.6	West-Central
Semi-terrestrial – arboreal clades	7.2	7.6	West-Central
***C. hamlyni* – arboreal clade**	6.0	6.2	West-Central
C. mona – C. neglectus	5.5	5.5	West Africa
C. neglectus + C. mona – C. diana + C. cephus + C. nictitans	5.4	6.0	West Africa
Allochrocebus + Erythrocebus – Chlorocebus	5.0	5.5	West Africa
G. matschiei	5.0	8.0	Central
C. diana – C. cephus + C. nictitans	5.0	5.2	West-Central
Allochrocebus - Erythrocebus	5.0	4.5	West Africa
C. cephus – C. nictitans	4.0	2.9	West Africa
Papio – Theropithecus	3.75	3.75	East-Central
***C. cephus* speciation**	3.6	3.5	West Africa
***Otolemur* spp.**	3.5	7.0	East
C. mona – C. pogonias	3.0	3.0	West Africa
C. a. djamdjamensis	2.8	2.8	Northeast
***Paragalago* spp.**	2.5	11	East
***C. cephus* speciation**	2.45	2.45	West Africa
C. mitis – C. nictitans	2.4	2.4	West-Central
***C. pogonias* speciation**	2.2	2.2	West-Central
***Pan* speciation**	2.0	2.0	West-Central
Papio kindae	1.7	1.7	South-Central
G. gallarum	1.5	2.0	East
P. ursinus* – other *Papio	1.3	2.5	South
G. moholi – G. senegalensis	1.0	1.0	East-Central
***Chlorocebus* speciation**	1.0	3.5	West-Central
Northern – southern *Papio*	0.9	2.3	Central
Papio ursinus – P. cynocephalus	0.9	1.5	East-Central
C. a. sabaeus* – other *Chlorocebus	0.531	3.5	West-Central
***C. nictitans/mitis* speciation**	0.5	2.4	West-Central
Western – eastern *Papio*	0.5	1.75	Central
C. a. aethiops	0.446	1.65	Northeast
C. a. tantalus	0.265	2.1	Central
P. anubis – P. hamadryas	0.25	0.25	Northeast
C. a. cynosuros – C. a. pygerythrus	0.129	2.0	South-Central

In Table 5.8, Cenozoic epochs are coloured successively in shades of violet (Eocene), lavender (Miocene), blue (Pliocene) and pink (Pleistocene - Holocene). The estimated geographical foci of these lineage divergences are coloured in shades of green, yellow and orange, with dark green designating West Africa, bright lime green describing West-Central Africa, light green identifying the regions denoted as Central, South-Central and East-Central Africa, and butter yellow coinciding with East Africa. The orange cells mark the only major divergences that occurred in South and South-Central Africa, i.e., the early splits of *Papio ursinus* and *P. kindae* from the other *Papio* species. These same colours are mapped onto a palaeo-globe reflecting the reconstructed African topography 30 Ma (Figure 5.10).

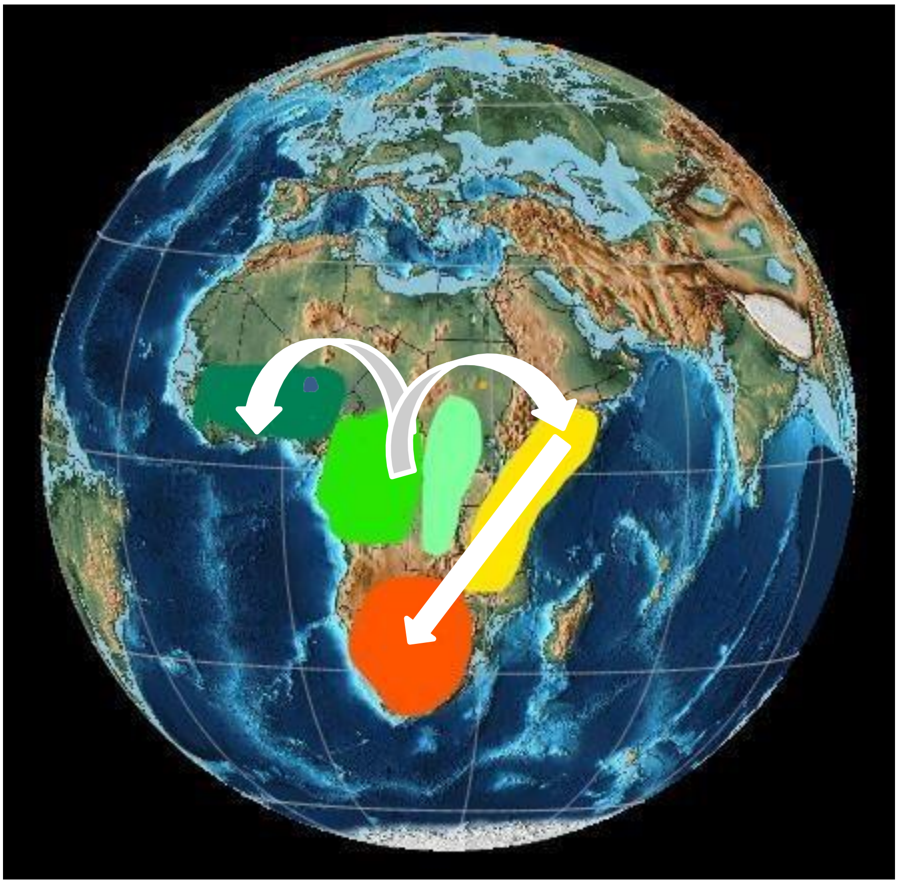


Figure 5.10. Palaeo-map 30 Ma constructed using Gplate, illustrating the likely geographical origins of African primate groups. On the basis of current distributions, the earliest divergences of major clades occurred in West-Central Africa (bright lime green), and then radiated towards the west, centre and east. The clade that originated in the south (baboons) probably derived originally from East Africa, as the sister genera *Papio* and *Theropithecus* occur in both regions. These separations coincide with major tectonic structures related to the Cameroon Volcanic Line and EARS, and the Congo-Kalahari watershed.

In order to compare more precisely the relative timing of lineage divergences across the five focal primate clades, I plotted a cumulative graph of minimum and maximum nodal divergence dates (Figure 5.11). Cumulative graphs allow the identification of changes in the frequencies of events – in this case, lineage divergence events – by the presence of inflection points on the curve.

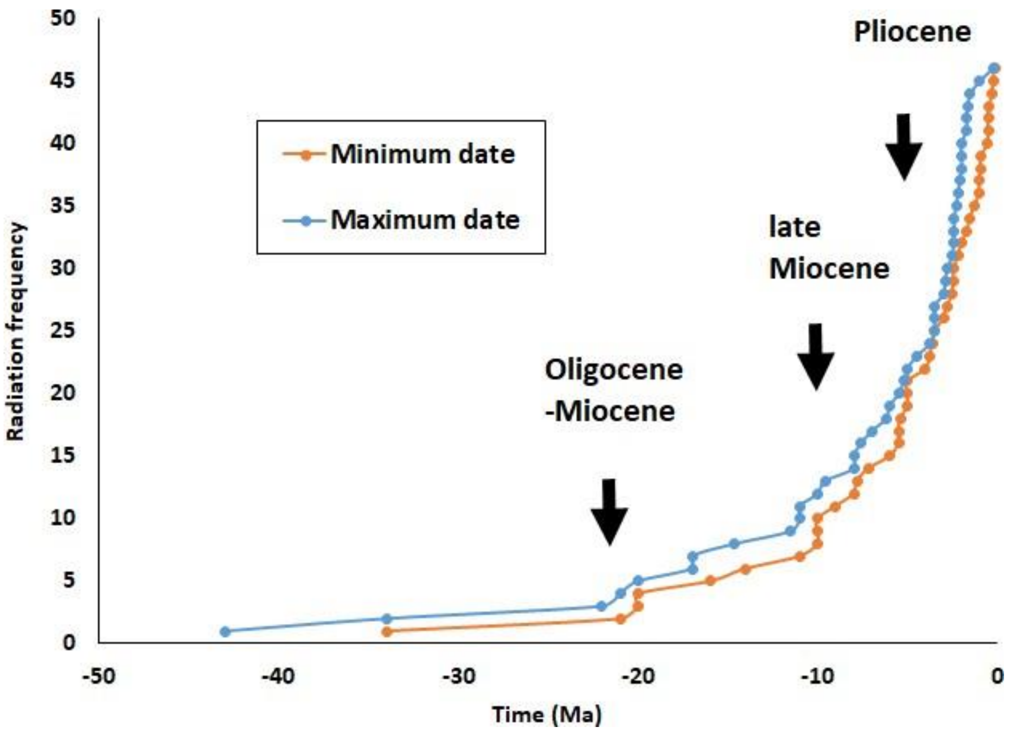


Figure 5.11. Cumulative frequencies of minimal and maximal estimates of nodal divergence dates extracted from the phylogenies of primate clades studied in this analysis. Three major inflections are indicated (arrows): (1) Oligocene-Miocene (~22 Ma); (2) late Miocene (~10 Ma); and (3) Pliocene (~5 Ma). The two oldest divergences are more obvious in the minimal estimates, while the third, at the Pliocene-Pleistocene boundary, is more evident in the maximal dates.

Three major inflexion points were identified. The Oligocene-Miocene transition (22 – 20 Ma) encompasses both the split between lesser and great apes (Hylobatidae and Hominidae), which is likely to have occurred in South-east Asia, and the early divergences among lorisoid primate lineages in Africa. The two slow-moving potto lineages, the common pottos (*Perodicticus*) and the golden pottos (*Arctocebus*), diverged from one another around this time. All of the early lorisoid divergences, including the end-Eocene divergence of the needle-clawed galagos (*Euoticus*), occurred in West-Central Africa, in the western part of the Congo Basin, which appears to have been the heart of early primate evolution in Africa.

The second concentration of lineage divergences occurred in the late Miocene, 11 - 7 Ma. This inflection point includes the divergence of the gorillas from the human-chimpanzee clade, followed by the chimp-human split some 2 Ma later. It also marks the beginning of the cercopithecin (guenon) radiation, and most notably, the divergence of the semi-terrestrial cercopithecin genera (*Allochrocebus*, *Erythrocebus* and *Chlorocebus*) from the arboreal genera, according to nDNA analyses. The geographical focus of all of these events is within the Congo Basin, distributed across this extensive area from the western to the eastern parts. Following the earliest radiations, populations expanded from west-central Africa both to the west and to the east, often speciating and they did so.

The third inflection point occurs around the Pliocene-Pleistocene boundary, 3 - 2 Ma. These younger divergence events span the west-east breadth of Africa, embracing an even greater geographical area than the late Miocene divergence events, including later elements of the lorisoid (specifically, galagid) radiation, as well as most of the extensive cercopithecin diversification.

All three of these periods of more intense diversification coincided with climatic aridification and the fragmentation of central African forests, and influenced diversification rates in the African lorisoids, hominoids and cercopithecoids. The two semi-terrestrial clades, the savanna monkeys (*Chlorocebus*) and the baboons (*Papio*), underwent their radiations between the late Pliocene and the Pleistocene (3.5 – 0.129 Ma for *Chlorocebus*; 2.5 – 0.25 Ma for *Papio*). The vervet monkey radiation therefore appears to have started prior to the baboon radiation, but while *Chlorocebus* diverged from its relatives in West-Central Africa and expanded from this point (westwards, eastwards and southwards), *Papio* shows a different biogeographic pattern. On the basis of the distributions of living species of *Papio* and its sister taxon, *Theropithecus*, the divergence of these two lineages at 3.75 Ma may have occurred in East-Central Africa (see Table 5.8), although the oldest lineage splits within *Papio* occurred much further south, while later divergences occurred after the genus had spread northwards and westwards.

5.2.2. Comparison of molecular divergence dates with palaeoclimatic and tectonic events

The earliest divergence among the living primate clades is the ~40 Ma divergence between lorisids and galagids in Central-West Africa, followed by the divergence of the needle-clawed galagos, *Euoticus*, 32 Ma in the same region (see section 5.1.1 and Figure 5.1). This region of Africa underwent substantial structural change starting around 34 Ma, with collapse and flushing of the Congo Basin sediments, leading to caving and badland topography (Guillocheau et al. 2015; Linol et al. 2015, 2019). This event resulted in both more relief and more humidity in Central Africa, and probably saw the emergence of more varied habitats and thus new selective pressures on organisms.

Table 3.1 (p. 29) shows the spatial and temporal distributions of the sequence of tectonic events that led to the modern EARS topography. The pattern is a highly complex one, with coeval rifting events occurring across wide geographic areas. Nevertheless, the overall patterns seen in this table and Figure 5.10, which maps the likely area of origin and subsequent spread of primates across Africa, have common features. Four of the five non-human primate clades studied here have their oldest lineages originating north of the equator. For those that dispersed eastwards towards the rift, their diversification patterns reflect the relative ages of rift formation, staring in the north and moving southwards, with only *Papio* radiating in the opposite direction. The complexity of topography relates directly to how terrestrial animals experience changes in climate and vegetation (Cracraft 1985). Animals living in areas with complex geomorphology are more likely to be trapped under changing environments – by mountains, rivers or inhospitable terrain – and subject to novel pressures of natural selection than those who can simply move with or track their preferred environments as they shift across the landmasses. Hence, palaeoclimatic and palaeovegetational changes are more intense in areas where topography changes dramatically over small distances (Cracraft 1985). As a consequence, the question is not whether tectonic events or palaeoclimatic events exert more control over biological diversification, but the fact that these two forces act in synergy with one another.

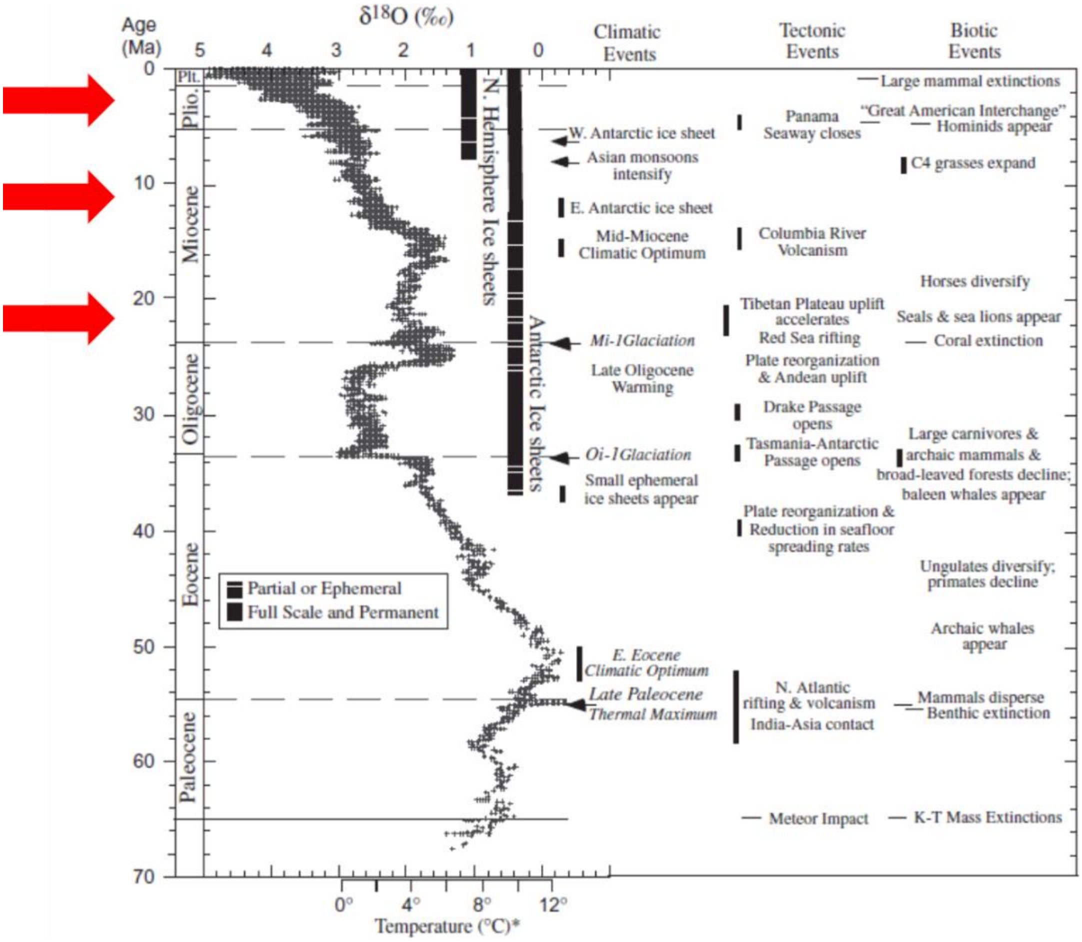


Figure 5.12. Representation of the synergistic interaction of tectonic events and global climatic changes in the Cenozoic, estimated from studies of stable isotopes in marine foraminifera (Zachos et al. 2001). The red arrows mark the three episodes of more intense diversification among African primate lineages demonstrated in Figure 5.11.

The fit between periods of enhanced diversification within the focal primate clades and global tectonic and climatic change during the Cenozoic is not close, but there is a clear staggered relationship in terms of older radiations. The divergence peak at 22 – 20 Ma follows late Oligocene warming and the 11 – 8 Ma peak follows the Mid-Miocene Climatic Optimum (Figure 5-12). The Plio-Pleistocene boundary peak at 3-2 Ma, however, occurs just before the temperature increase at 1.8 Ma. Given the uncertainties related to molecular and geological dates, the age differences may simply be a consequence of the coarse resolution of the data. Alternatively, the relationship between speciation and palaeoclimatic changes may be much looser than theory predicts, and there may be more regional tectonic controls within the EARS than previously envisaged.

CHAPTER SIX: LINKING NON-HUMAN PRIMATE EVOLUTION TO HUMAN EVOLUTION IN AFRICA

While most of the non-human primate clades that evolved alongside hominins in Africa show a degree of extant diversity, allowing us to reconstruct their evolutionary histories using molecular sequencing and clock methods to augment the limited fossil record, the hominin clade is represented today by one surviving species. The fossil record, therefore, is the major source of information about the history of our own clade, while the archaeological record provides additional information regarding the development and use of tools, patterns of settlement and dispersal, and diet of hominins (Potts 1996). In this chapter, I investigate the African hominin fossil record with reference to the information summarised in Chapter 5 relating to non-human primate evolution.

6.1 The hominin fossil record in Africa

The African hominin fossil record is discontinuous and often sparse, but it dates back in time to shortly after the molecular clock estimate of the *Homo-Pan* split at 8 Ma (Table 5.2, Figure 5.4). Based on the distribution of living African apes, this event appears to have occurred in central Africa, either in or bordering the Congo Basin. I summarise information regarding the seven hominin genera that have been recovered from African fossil sites below.

6.1.1. Sahelanthropus

The oldest putative hominin fossil taxon, *Sahelanthropus tchadensis*, is based largely on a single, almost complete but heavily distorted fossil cranium (Brunet et al. 2002), although the hypodigm now also contains fragments of an upper and lower jaw, several teeth and a partial left femur, identified recently (Macchiarelli et al. 2020). The fossils were discovered in northern Chad and dated at 7 Ma, which fits with the assumption that the hominins diverged from the lineage leading to *Pan* species around 8 Ma in central Africa. The cranium is relatively small with an ape-sized braincase, and has an orthognathic facial profile; i.e., there is little nasal prognathism or snout development. The basicranium is nevertheless long and narrow. The dental arch is narrow and U-shaped, as in apes, and like them, it has a large canine fossa. The orbits are separated by a wide interorbital pillar, and are surmounted by a thick, continuous supraorbital torus. Behind the orbits there is a marked postorbital constriction, as is to be expected in a small-brained hominid. At the back of the cranium there is a small sagittal crest, but the nuchal crest is large. Many of the features are ape-like, but Brunet et al. (2002) proposed that the species was bipedal based on the somewhat forward position of the foramen magnum. Macchiarelli et al. (2020), however, rejected this hypothesis after examining the partial femur, and questioned the hominin status of *Sahelanthropus*. The proposed habitat occupied by this genus includes forests and savanna woodlands with open areas of freshwater.

6.1.2. Orrorin

The genus *Orrorin* similarly comprises a single species, *O. tugenensis*, recovered from 6.1 – 5.7 Ma sediments in the Tugen Hills in central Kenya (Senut et al. 2001). The type specimen is a mandibular fragment with three lower molars, and the hypodigm consists of 13 fossils representing at least 5 individuals, including two well-preserved femora. *Orrorin* has been interpreted as bipedal from the structure of the proximal femur: i.e., a spherical head rotated anteriorly and a long neck. Other parts of the skeleton show ape-like characteristics, including long, curved fingers and ape-like canines and premolars. *Orrorin* also had thick-enamelled central incisors and molars, as found in apes, but the dentition is small relative to body size, which was approximately that of a chimpanzee (Hartwig 2002). No cranial elements have been found, and hence nothing is known about the skull. The habitat proposed for *Orrorin* is similar to that reconstructed for *Sahelanthropus* (Jacobs 2002).

6.1.3 Ardipithecus

Fossils of this genus have been included in two distinct species, *Ardipithecus ramidus* (5.8 - 4.4 Ma) (White et al. 2009) and *A. kadabba* (5.8 – 5.5 Ma) (Haile-Selassie and WoldeGabriel 2009), both discovered in late Miocene strata of the middle Awash River valley of the Afar desert region of Ethiopia. The type specimen of *A. ramidus* is made up of the dentition of a single 4.4 Ma individual, but the hypodigm also includes the partial skeleton of a young adult female comprising 125 components, including parts of the skull, pelvis, leg, foot and forearm (White et al. 2009). *Ardipithecus kadabba* is represented by fragmentary fossils from at least five individuals, including a lower jaw, teeth and postcranial elements (Haile-Selassie and WoldeGabriel 2009). The presence of slightly more ancient features in the *A. kadabba* fossils has led to the suggestion that this species was the direct antecedent to *A. ramidus*. *Ardipithecus* species have a mosaic morphology, sharing some features with later hominins and others with *Orrorin*, *Sahelanthropus*, and even apes. Their canines were incisiform and did not project far beyond the incisor tooth row, but they were nevertheless more projecting than those of *Australopithecus* species. Their postcanine teeth, however, were not as large as those of *Australopithecus*, and more similar to those of later *Homo* species. Like most hominins, *Ardipithecus* had relatively thin tooth enamel. Like *Orrorin* and *Australopithecus* individuals, members of *Ardipithecus* were similar in body size to living chimpanzees (Hartwig 2002). Their postcranial anatomy indicates that they were not obligate bipeds, but facultatively so, and partially arboreal, climbing easily in trees with the aid of an opposable big toe. They inhabited forests and wooded savannas near fresh water.

6.1.4 Australopithecus

Australopithecus was first described by the South African anatomist Raymond Dart (1925) from the facial skeleton and lower jaw with partial deciduous dentition, and the endocast of a juvenile specimen about 3 years of age. Just over two decades later, Robert Broom and John Robinson discovered an adult specimen of the taxon, STS 5, who is affectionately referred to as Mrs Ples. Since then, many more fossils of *A. africanus*, which lived in South Africa between 3.3 and 2.1 Ma, have been discovered, including dental, cranial and postcranial material, allowing interpretation of the species' locomotion, behaviour and diet, as well as an estimated cranial capacity of 440 cm^3. While *A. africanus* was the first member of the genus to be described, it was not the oldest species of this lineage. *Australopithecus afarensis* was described by Johanson et al. (1978) from an almost complete adult mandible with teeth, found in Laetoli, Tanzania. Many more fossils have since been recovered and dated using geochronology from volcanic deposits, giving *A. afarensis* a time span of 3.7-2.9 Ma and a geographic range that includes Tanzania, Kenya, and Ethiopia. A 40% complete skeleton of the species was found at Hadar within the Afar depression, northern Ethiopia (Figure 3.2). The depression is also referred to as the Afar triangle, as it marks the boundaries of three tectonic plates (see section 3.3.1, p. 30). Nicknamed Lucy, the skeleton showed both adaptations to bipedal locomotion and more unique australopith features. For example, its forelimbs were relatively long relative to the lower limbs, and its iliac blades were turned outwards. Like other *Australopithecus* species, the stature of *A. afarensis* is estimated to have been 1.2 – 1.5 m in height, with an adult body weight between 30 and 55 kg. Sexual size dimorphism is likely to have been greater than in modern *Pan* or *Homo*, but less than in modern *Gorilla*, and brain size ranged from 350 to 600 cm^3. The incisors were broad and chimp-like, and the canines extended well beyond the occlusal margins of the other teeth, with a large diastema between the lower canines and cheek teeth to accommodate the upper canines. The postcanine dentition was megadont with thick enamel, and the face was prognathic (Hartwig 2002).

Lucy's claim to be a member of the oldest known *Australopithecus* species was short-lived, undermined by the description of *A. anamensis* by Maeve Leakey and coworkers (1995) from an adult mandible with dentition discovered at Allia Bay in northern Kenya (West Turkana). While the lower jaw is decidedly ape-like, with large canines and and parallel tooth rows, fragments of limb bones suggest it had a postcranial structure that was capable of bipedal locomotion. The hypodigm now consists of almost 100 fossils from at least 20 individuals, distributed from West Turkana to Ethiopia over a time span of 4.2-3.9 Ma (Hartwig 2002). A second *Australopithecus* species that showed this ape-like skull matched with a hominin postcranium was *A. garhi*, described by Asfaw et al. (1999) from 2.5 Ma beds preserved in Bouri, in the Afar depression (Figure 3.2). The species is represented by a partial skull and partial skeleton, plus several other fragments. The cranium has a crested vault, a palate with dentition, and a cranial capacity of 450 cm^3. The face is prognathic, as in *A. afarensis*. The remains date to 2.6-2.5 Ma. In addition to Bouri, they have been recovered from Baringo Chemeron, Kenya and Omo Shungura, Ethiopia (Hartwig 2002; see Figure 3.3). An australopith species known from three partial mandibles and some teeth, *A. bahrelghazali*, apparently lived 3.5 Ma in Chad, north-central Africa. Little is known about this species, and its main significance lies in the fact that it extends the range of australopiths much further west than East Africa (Tattersall and Schwartz 2000).

One of two hominins discovered more recently in South Africa (2008) is *Australopithecus sediba.* The specific name means ‘fountain’ or ‘wellspring’ in the seSotho language. The remains were found in Malapa Cave, in the Cradle of Human Kind, Gauteng Province, and are estimated to be 1.98 Ma based on a combination of palaeomagnetism, uranium-lead dating and fauna found at the site. This time frame would have made the taxon contemporaneous with *Paranthropus robustus* and early *Homo* (*H. ergaster*). The hypodigm includes two partial skeletons, one (the holotype) is a juvenile, and the second, that of an adult female (paratype). The holotype is also represented by a partial cranium and a fragmented mandible, while the paratype includes isolated maxillary teeth and a partial mandible. The distorted cranium indicates a cranial capacity of 420 cm^3. The postorbital constriction is slight (relatively large brain size), and there is no nuchal cresting, but these characters could relate to the young age of the specimen when it died. Even so, the skull had marked supraorbital torus. The face was not strongly prognathic, although the canines protruded beyond the cheek tooth row. The dental arcade is parabolic, and the mandibular symphysis is vertical (Berger et al. 2010). The postcranial elements include fore- and hindlimb bones, vertebrae and ribs, and parts of the pelvis. These elements show a mix of *Australopithecus* and *Homo* characteristics. From the feet to the abdomen, there is evidence that the species habitually walked upright. However, from the thorax to the skull, the species is similar to other australopiths, and the arms are relatively long. It may be a descendent of *A. africanus* (Smithsonian Institution: humanorigins/si/edu).

6.1.5 Kenyanthropus

The only species within this genus, discovered in West Turkana in 1999, is *Kenyanthropus platyops,* which lived 3.5-3.3 Ma according to geochronological dating of tuff layers above and below the fossils. It would therefore have been coeval with *Australopithecus afarensis*. Its specific epithet derives from its relatively flat face (lack of prognathism), small molars, and an anterior placement of the zygomatic processes. Its brain size was smaller than those of most australopiths, but it was capable of bipedal locomotion (Leakey et al. 2001).

6.1.6 Paranthropus

The oldest known member of the genus *Paranthropus*, *P. aethiopicus*, was first described by Arambourg and Coppens (1968) from an edentulous partial adult mandible. The new taxon did not have much credibility until the discovery of the “Black Skull” KNM-WT 17000 on the western shore of Lake Turkana by Walker in 1985 (Walker et al. 1986). The name comes from the fact that the skull has been mineralised to a coal-black colour (Tattersall and Schwartz 2000). The species is known from 2.7-2.3 Ma sediments in Kenya and the Omo Valley, Ethiopia. No postcranial elements are known. The skull’s cranial capacity is relatively small (420 cm^3). In all paranthropines, the skull and mandible are extremely robust and the face is dished, but while the other species had small incisors relative to their molars and premolars, *P. aethiopicus* had relatively larger anterior teeth. All *Paranthropus* species had molarised premolars, extending the occlusal row (Hartwig 2002).

Two other species have been allocated to the genus *Paranthropus*: *P. boisei* (nicknamed Zinj for *Zinjanthropus*, 2.5 – 1.15 Ma), discovered in 1959 by Mary Leakey in Olduvai Gorge, Tanzania; and *P. robustus* from South Africa (2.3 – 0.9 Ma). The South African species was the most recent taxon to be found in the fossil record, but the first robust australopith to be discovered. The genus was named by Broom (1938). *Paranthropus* boisei and *P. robustus* both show relatively short, dished facial profiles and massive cheek teeth and mandibles. Several crania show a short sagittal crest at the back of the skull, supporting the interpretation that they had very large chewing muscles. They are assumed to have lived on a diet of roots and tubers, and possibly seeds (Tattersall and Schwartz 2000). They were bipedal, weighed approximately 40–50 kg, and coexisted in woodland habitats with *Australopithecus africanus*, *Homo habilis* and even *H. ergaster.*

6.1.7 Homo

Our genus was described by Linnaeus (1758), and is likely to have emerged around 2.5 Ma, contemporaneous with the earliest stone tools (Tattersall and Schwartz 2000). Cranial capacity varies with stature, but is always large relative to body size in *Homo* species (Gould 1980), and there is limited postorbital constriction or lower facial prognathism. The foramen magnum is situated anteriorly, almost midway along the cranial base, and the vault is high. The species has narrow tooth crowns, particularly in the mandibular premolars. The molar tooth row is short, and although molar size is variable, they are not broad buccolingually, as in some australopiths (Hartwig 2002).

Homo habilis was described by Leakey et al. (1964) from a mandible with teeth, upper molar, parietals and possibly hand bones of a juvenile individual from Olduvai Gorge. The species lived 2.3-1.6 Ma across a wide geographical range that encompassed Omo and Hadar, Ethiopia; Olduvai Gorge, Tanzania; East Lake Turkana, Kenya; and Sterkfontein, South Africa. The cranial capacity (600 cm^3) is greater than in *Australopithecus* species, but smaller than in *H. erectus* (800 cm^3). The mandibles and maxillae are smaller than those of *Australopithecus*, but within the range of *H. erectus* and *H. sapiens*. There is an incipient but variable supraorbital torus. All teeth show buccolingual narrowing and mesiodistal elongation, especially the mandibular molars and premolars (Hartwig 2002). *Homo habilis* was named "handy man", because of the species was thought to have been the first maker of stone tools, although this cannot be confirmed. Susman (1988) proposed that *Paranthropus* could have fashioned and used tools.

Homo habilis became more and more of a waste-basket taxon as more hominin fossils from this time period were collected. From 1.9 Ma old deposits, at least four morphotypes were identified and placed within this taxon. *Homo rudolfensis* was described by Alexeev (1986) from an edentulous adult cranium from Koobi Fora, Kenya. It had a larger cranial capacity than *H. habilis*, and the skull had a more orthognathic lower face and a larger palate. It also had relatively and absolutely large upper anterior alveoli compared to *H. habilis* (Hartwig 2002), implying larger anterior teeth, and more modern postcranial proportions (Tattersall and Schwartz 2000). The former highly variable *H. habilis* hypodigm has been loosely sorted between these two species.

The origin of *Homo* around 2.5 Ma coincided with a significant cooling and drying trend in Africa, brought on by the expansion of the Arctic ice sheet 2.8–2.5 Ma (Figure 5.11). The fossil record shows that many forest antelope species became rare or extinct, and were replaced by larger grassland feeders. By 2.3 Ma, the Pleistocene climatic oscillations between glacial and interglacial cycles intensified (Vrba 1993; Tattersall and Schwartz 2000). Early *Homo* species like *H. habilis* would have been largely confined to woodlands, although *H. rudolfensis*, with its more modern postcranium, was probably associated with marginal areas bordering on grasslands (Tattersall and Schwartz 2000). A comprehensive study of the existing vegetation of the Koobi Fora region in Kenya has been undertaken by Mbaluka and Brown (2016).

Later species, like *H. erectus* and *H. ergaster*, were obligate bipeds, and they evolved during this period of rapid climatic fluctuations. *Homo erectus* was one of the first *Homo* species described, but not from Africa: in 1891-2, Dubois described the species from an adult partial cranium from Java, Indonesia (Alink et al. 2016). In the 20th century, specimens attributed to this taxon were discovered over a wide area in Africa in deposits ranging in age from 1.8 to 0.3 Ma, but, like *H. habilis*, fossils attributed to *H. erectus* show wide morphological variation, particularly between the Asian and African forms. As a result, some researchers choose to refer to African '*H. erectus*' as *H. ergaster*, although even this subset of fossils is likely to include more than one species. *Homo ergaster* has been found in East and West Turkana, the Baringo basin and Lainyamok, Kenya; in Olduvai Gorge, Tanzania; Swartkrans, South Africa; Melka Kunture and Omo, Ethiopia; Tighennif, Algeria; and Thomas Quarries, Salè and Sidi Abderrahman, in Morroco. The taxon has a long, low skull with its greatest breadth toward the cranial base, a pronounced supraorbital torus on the frontal bone and a strong occipital torus at the rear, and a significantly greater degree of postorbital constriction than *H. sapiens*. The bones of the cranial vault are thick, and cranial capacity ranges from 700 to 1300 cm^3. The mandibular rami are broad, and the bicondylar breadth also. The chin is receding, and the upper central incisors are shovel shaped. The upper and lower limb proportions were similar to modern humans (Hartwig 2002).

The tools found associated with *H. ergaster* fossils (but not with Asian *H. erectus*) are much more sophisticated than the Oldawan stone tools associated with early *Homo*. This taxon developed the teardrop-shaped Acheulean handaxes, never found in China or Indonesia. The most intriguing *H. ergaster* specimen is the near-complete skeleton of a youth aged 9 to 12 years at death, known as the Nariokotome boy. At his young age he was already 160 cm tall, and would have reached 2 m as an adult. His body proportions were modern. This group of obligate bipeds may have been the first to leave Africa for Europe and Asia (Tattersall and Schwartz 2000).

The most recent *Homo* species to be discovered in Africa was *Homo naledi*, recovered from the Rising Star Cave in the Cradle of Human Kind (Berger et al. 2015). The hypodigm contains ~1700 fossils representative of almost 20 individuals, and includes cranial and mandibular material from at least five adults. Like most other *Homo* species, *H. naledi* combines ancient and modern traits that yield a mosaic morphology. The cranium lacks well-developed crests, the mandibles are gracile, and the mandibular molars are buccolingually narrow, as in humans. The postorbital constriction is slight, but the frontal bone has a well-developed supraorbital torus. The shoulder and pelvis resemble australopiths (Berger et al. 2015). *Homo naledi* had a relatively long hallux and, like humans, a long thumb: apes, which use their hands for climbing, have short thumbs. The most interesting aspect of this species, though, is its young age, overlapping with early *H. sapiens*. The most recent age estimate is 335,000 to 236,000 years ago (Dirks et al. 2017), while archaeological and palaeontological evidence indicates that *H. sapiens* has been in existence for > 300,000 years (Hublin et al. 2017). Despite the large number of fossil fragments that have been found, little is known of the species' ecology.

6.2. Co-occurrence of hominin and non-human primates at fossil sites

The fact that hominins evolved not only figuratively but literally side-by-side with other African primates is evident from the fossil record. At several sites from which hominins have been recovered, the remains of a variety of non-human primates, from lorisoids to cercopithecoids and other hominoids, have also been unearthed (Tables 6.1 to 6.4). The presence of these species provides environmental context information for the sites and for the hominin species buried there.

Table 6.1. List of primate and hominin fossils found in the Ethiopian region of the East African Rift System. The yellow cells mark the period after the 2.5 Ma evolution of *Homo.*

Genus/Species	Location	Elevation m (a.s.l.)	GPS co-ordinates	Age (Ma)	Reference
Ardipithecus ramidus	Middle Awash	2376 m	9.99996, 39.9998	5.8-4.4	White et al. 2009
Pliopapio alemui	Middle Awash Afar region	2068 m	11.6446, 38.7897	5.7-4.2	Werdelin and Sanders 2010
Australopithecus afarensis	Hadar	1671 m	9.1215, 36.0005	4.2-3.0	Johanson et al. 1978
Parapapio jonesi	Hadar	1671 m	9.1215, 36.0005	3.5-3.0	Johanson et al. 1976
Australopithecus garhi	Middle Awash	2376 m	9.99996, 39.9998	2.5	Asfaw et al. 1999
Australopithecus boisei	Omo formation	645 m	3.85, 35.756	2.3	Harris et al. 1988
	Konso	1605 m	5.25, 37.5	1.4	Suwa et al. 1997
Papio hamadryas	Middle Awash Afar region	2068 m	11.6446, 38.7897	Pleistocene	Kalb et al. 1982

Table 6.2. List of primate and hominin fossils found in the Kenyan region of the East African Rift System. Yellow cells mark the period after the 2.5 Ma evolution of *Homo.*

Genus/Species	Location	Elevation m (a.s.l.)	GPS co-ordinates	Age (Ma)	Reference
Progalago	Lake Victoria Songhor	1178 m	-0.1833, 35.2579	19	Werdelin and Sanders 2010
Victoriapithecus macinessi	Maboko Island	1135 m	-0.1639, 34.5922	16 - 14.7	Benefit 1999
Komba	Maboko Island	1135 m	-0.1639, 34.5922	15	Retallack et al. 2002
Parapapio lothagamensis	Nachukui formation Lothagam	854 m	4.0627, 35.8777	7.4-5	Werdelin and Sanders 2010
Orrorin tugenensis	Lukeino formation Tugen Hills	1274 m	0.5, 35.6667	6	Senut et al. 2001
Kenyathropus platyops	West Turkana	634 m	3.4562, 35.1471	3.5	Leakey et al. 2001
Parapapio whitei	West Turkana	634 m	3.4562, 35.1471	3.36-2.35	Hartwig 2002
Paranthropus aethiopicus	Lake Turkana	634 m	3.4562, 35.1471	2.7-2.3	Smithsonian Institution
Homo rudolfensis	Koobi Fora	546 m	3.6362, 36.3475	1.9-1.8	Argue 2017
Homo erectus	Koobi Fora	546 m	3.6362, 36.3475	1.6	Baab 2016

Table 6.3. A list of primate fossils found in the Tanzanian region of the East African Rift System. Again, the yellow cells describe the period after 2.5 Ma.

Genus/Species	Location	Elevation metres (a.s.l)	GPS co-ordinates	Age (Ma)	Reference
Australopithecus afarensis	Laetoli	1644 m	-3.2249, 351896	4.2-3.9	Johanson et al. 1978
Parapapio ado	Laetoli	1644 m	-3.2249, 35.1896	4.1-3.49	Werdelin and Sanders 2010
Papio izodi	Laetoli	1644 m	-3.2249, 35.1896	3.3-2.6	McKee 1993
Homo habilis	Olduvai Gorge	1646 m	-2.6667, 35.3579	2.4-1.4	Leakey et al. 1964
Paranthropus boisei	Olduvai Gorge	1646 m	-2.6667, 35.3579	1.75	Leakey 1959
Papio hamadryas	Olduvai Gorge	1646 m	-2.6667, 35.3579	Pleistocene	Werdelin and Sanders 2010

Table 6.4. A list of primate fossils found in South African hominin sites. All sites include the period at or after 2.5 Ma.

Genus/species	Location	Elevation Metres (a.s.l)	GPS co-ordinates	Age (Ma)	References
Parapapio broomi	Sterkfontein	1708 m	-26.0168, 27.7314	Pliocene	Werdelin and Sanders 2010
Parapapio whitei	Makapansgat	1118 m	-25.2389, 28.0852	3.36-2.35	Hartwig 2002
Papio robinsoni	Swartkrans	2340 m	-26.0189, 27.7163	Pleistocene	Hartwig 2002
Papio angusticeps	Malapa	1480 m	-24.9522. 27.4918	2.026- 2.36	Gilbert et al. 2015
Papio hamadryas	Sterkfontein	1708 m	-26.0168, 27.7314	Pleistocene	Werdelin and Sanders 2010
Parapapio jonesi	Makapansgat	1118 m	-25.2389, 28.0852	Pliocene	Werdelin and Sanders 2010
Parapapio antiquus	Taung	1086 m	-27.5569, 24.7428	Plio-Pleistocene	Hartwig 2002
Papio izodi	Taung	1086 m	-27.5569, 24.7428	Plio-Pleistocene	McKee 1993
Australopithecus sediba	Malapa cave	1442 m	-25.5342, 27.4805	1.98	Berger et al. 2010
Australopithecus africanus	Taung	1086 m	-27.5518, 24.7662	3-2	Grine 2013
Paranthropus robustus	Kromdraai	1122 m	-25.4833, 28.2667	2.27-0.87	Steininger et al. 2008
Homo naledi	Cradle of humankind	1480 m	-25.9254, 27.7674	335-236 ka	Berger et al. 2015

6.3 Discussion

The objectives of my research project were to study the correlations and interactions of diverse environmental forces (tectonism and the creation of the East African physical geography; contemporaneous changes in climate and vegetation) with the patterns of evolution and diversification among five extant clades of non-human primates that evolved alongside hominins in Africa. The impact of geological and palaeoclimatic events on human evolutionary history are difficult to study directly, because there is only a single surviving species in this clade. All of the taxa that came before *Homo sapiens* are known from fragmentary fossils, the relationships of which are difficult to reconstruct with any certainty. Ancient DNA data exist only at the very tips of the tree, for our own species and for *Homo neanderthalensis*. In order to overcome this difficulty, I chose to investigate the timing and structure of clade diversification of the African Lorisoidea (40 to 1 Ma), the Hominoidea (20 to 0.3 Ma), the Cercopithecini (15 to 1 Ma), the genus *Chlorocebus* (3.5 to 1.65 Ma) and the genus *Papio* (2.5 to 0.25 Ma). The lorioids, hominoids and cercopithecins are largely arboreal, while *Chlorocebus* and *Papio* are semi-terrestrial.

I conducted an extensive literature review and tabulated information regarding maximum and minimum divergence ages, the major tectonic events that restructured Africa's geological surface over the past 40 Ma, the palaeoclimatic regimes that characterised the Cenozoic epochs from the middle Eocene to the present, and the potential interaction and mutual influence of these aspects of Africa's evolutionary history. My objective was to learn more about the history of hominin evolution in Africa, to test the savanna hypothesis which posits that a bipedal, terrestrial lifestyle was adapted by hominins who transitioned from an arboreal lifestyle when forests were a prominent feature of the landscape to a more terrestrial lifestyle with the spread of savanna grasslands. I also explored Vrba's (1993) turnover-pulse hypothesis which posits that, if adaptation and speciation are driven by climatic, vegetational and tectonic changes, then major changes to the climate and ecosystems should cause rapid periods of extinction and speciation (pulses of biodiversity change) across multiple, diverse lineages of organisms.

Figure 6.1 is based on an image taken from Wichura et al. (2011), which demonstrates my approach to this project, although the only clade considered in this diagramme is that of the hominins. The picture I generated by comparing the environmental data with the history of non-human primates rendered additional, longer-term insights. The broad pattern of primate evolution demonstrates that four of the five primate clades I studied, including the hominoids, are likely to have originated in west-central Africa. The deepest lineages divergences can all be traced to this part of the continent, which is likely to have supported forest patches in the Palaeogene and early Neogene (Wichura et al. 2011). The pan-African rain forest was already present 20 Ma, the primates living during this time were the likes of *Rungwepithecus, Limnopithecus* and *Noropithecus*. The savanna expansion began 16 Ma, and the first C_4 plants emerged in Kenya approximately 15 Ma. Volcanism and rifting in central Kenya at 10 Ma, and in northern Tanzania around 6 Ma and at 4 Ma, may also have altered ecosystems. By the Pliocene, herbivorous mammals had mixed C_3-C_4 diets; at the Plio-Pleistocene boundary, the climate was dry.

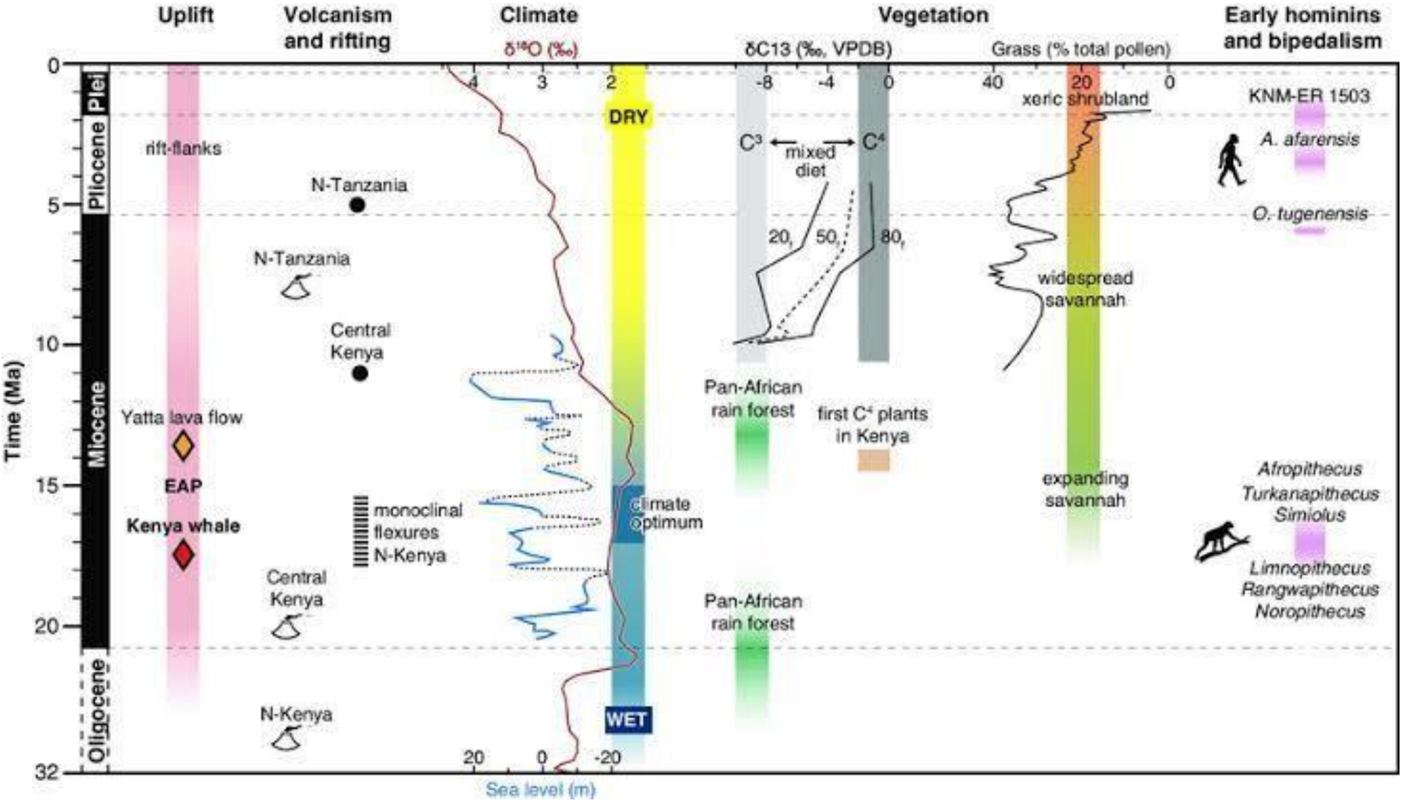


Figure 6.1. Chronostratigraphy from Wichura et al. (2011), depicting uplift, volcanism, climate change and palaeo-vegetation. Uplift data are taken from palaeo-altimetric data and correlated with major climatic and environmental shifts. Vegetation data are derived from herbivore teeth, carbon isotopes and fossil plant records, while climatic data are recorded in deep sea oxygen isotopes. Early Miocene apes were probably quadrupedal, while mid- to late Miocene apes likely included more suspensory hanging in their movements. Hominin bipedalism began around the end of the Miocene, ~6 Ma, but obligate bipeds are < 2 Ma.

6.3.1 Linking primate diversification to Cenozoic climates

The Eocene-Oligocene transition was a period of cooling and drying (Prothero 1994), driven by the first formation of ephemeral ice sheets on Antarctica (Lear et al. 2000; Zachos et al. 2001; Coxall et al. 2005; Bobe 2006) (see Figures 4.1 and 5.11). It also marked the beginning of uplift and rifting in the EARS, starting in Ethiopia, and moving progressively south (see Table 3.1). The only extant genus proposed to have evolved at this time is the needle-clawed galago (*Euoticus*), which is today restricted to forests in eastern Nigeria, Cameroon and Gabon (Pozzi 2016). Needle-clawed galagos are obligate gum-feeders, and adapted to spending long periods clinging to vertical tree trunks using their needle-claws while they scrape and gouge tree exudates. It is likely that obligate gum-feeding is related to periods of environmental unpredictably and increased seasonality. Gum is available in all seasons when other food sources (fruit, insects) may be rare (Génin et al. 2010). These ancient primates may have emerged after the collapse of the Congo Basin.

Although the extent of the central African forest at this time is not well characterised, indications are that the inland parts of the African continent were dry (Jacobs 2004; Bobe 2006; see section 4.2.2). However, the Eocene dry seasons were less severe than today (Jacobs 2004; Jacobs and Herendeen 2004), allowing the development of a vegetation similar to today's miombo woodland (see section 4.2.2). In north-eastern Africa in the Fayum depression, mangroves flourished during this transition, indicating more moist environments further north.

In accordance with the turnover-pulse hypothesis of Vrba (1993), my summary of primate divergence dates indicates three periods of higher diversification among the five primate clades. The first of these marks the transition from the Oligocene to the Miocene (23 Ma). During this period, the great apes diverged from the lesser apes, probably in Southeast Asia, where both great and lesser apes occur today. The two extant potto genera endemic to West-Central Africa, *Arctocebus* and *Perodicticus*, both of which are reliant on trees for their locomotion, also diverged around this time, probably because of a fragmentation of the central rain forest. The western dwarf galagos (*Galagoides*), also dependent on forests, apparently separated from the other taxa around this time.

The middle Miocene, 15 – 11 Ma, was a period of progressive drying and expansion of grasslands. The greater galago lineage (*Otolemur* + *Sciurocheirus*) diverged around this time, followed by the lesser and eastern dwarf galagos (*Galago* and *Paragalago*). Evidence of this progressive drying can be seen in fossil assemblages from the Tugen Hills in Kenya. At 12.6 Ma, the fossils indicate the presence of lowland forest vegetation and vertebrates in this area, whereas fossils recovered from lacustrine deposits dated at 6.8 Ma indicate woodland or dry forest. This change may also be due to tectonic processes uplifting the local topography. The first evidence of equids in the Tugen Hills is documented between 9.5 and 8.5 Ma, but other vertebrate fossils from this period show evidence of mixed vegetation regionally. Large herbivores appear to have shifted from C_3 to C_4 plant diets between 8.5 and 6.5 Ma. Grasses were part of the African landscapes since 64 Ma, but significant grassland expansion only began ~16 Ma, with them becoming a dominant feature around 8 Ma. Volcanism concomitantly progressed southward across the EARS (Figure 6.1).

The most active period of diversification among extant primate genera reflects this suite of changes in vegetation regimes, with most genera separating in the late Miocene, from 11 – 5 Ma. The tribes Papionini (baboons and mangabeys) and Cercopithecini (guenons) embarked on separate ecological trajectories at this time. Gorillas diverged from the *Pan-Homo* clade ~10 Ma. The arboreal guenons began their radiation ~9 to 7 Ma, with most of the major species-groups separating by 5 Ma. The semi-terrestrial clades diverged from the arboreal clades between 7.6 and 7.3 Ma.

The most terrestrial genera and species of primates, including *Erythrocebus*, *Cholorocebus*, *Papio* and *Homo* species, all emerged during the Plio-Pleistcene, at or after 5 Ma, when woodlands and savanna grasslands were a common feature of the East African landscapes. Aridification in Africa intensified 3.2 to 3.0 Ma with the beginning of glaciation in the northern hemisphere. The period from 2.3 to 0.01 Ma was characterised by increased climatic instability, with a succession of cold and dry phases alternating with hot and humid phases, and more rapid shifts in vegetation. The closure of savanna corridors during the humid phases is likely to have isolated baboon and vervet populations and led to the fixation of different morphologies. Baboon species even show differences in social organisation, which are likely to be linked to different habitat types. Cool and dry phases would have led to the shrinking and fragmentation of forests, and many speciation events occurred among arboreal primate lineages in the Pleistocene, including the more aboreal galagid genera and the cercopithecin species groups.

The *Chlorocebus* radiation began 3.5 to 0.53 Ma with a separation between West and East African clades, and expanding southwards. The genus *Papio*, however, appears to have done the opposite, with the oldest divergences occurring in the south 2.5 to 1.5 Ma, and later divergences (1.5 to 0.25 Ma) taking place further north. Ongoing hybridisation within these clades, however, complicates the estimation of divergence dates. The genus *Homo* appears to have emerged approximately 2.5 Ma: the early species (*H. habilis, H. rudolfensis*) had postcranial proportions much like australopiths, and were still relatively arboreal. *Homo ergaster* and *H. erectus* were obligate bipeds, and emerged around 1.8 Ma, after the onset of the Pleistocene climate oscillations. The most recently diverged species of galagids (2.0 – 1.0 Ma), *Galago moholi*, *G. gallarum* and *G. senegalensis*, are all associated with drier woodland habitats rather than forests.

The coincidence of increased rates of diversification across primate clades co-evolving in Africa provides support for Vrba's (1993) turnover-pulse hypothesis, which in turn posits that environmental change was a primary driver of speciation and extinction.

6.3.2 Linking palaeoclimatic regimes to Africa's tectonic history

Climate change is strongly associated with tectonic events, both at local and global scales. For instance, the global Cenozoic cooling events have been attributed to the uplift of Tibet and the closing of the Panama Isthmus. Tectonic events may change patterns of ocean circulation and sea temperatures, as well as watersheds and rainfall patterns. Climate change in East and southern Africa, in particular, has been linked to the formation and propagation of the EARS. Volcanic activity began 45 Ma in Ethiopia and reached northern Kenya 33 Ma. By 15 to 8 Ma, rifting had spread to the southern segments of the Kenyan rift and to Tanzania, further intensifying the topography. Lake basins first formed in the northern parts of the EARS because of the southward propagation of rifting and magmatic activity. The fluvio-lacustrine deposits of the Afar, Omo-Turkana and Baringo Borgoria basins were preserved during the mid- to late Miocene, while the lacustrine deposits of the Kenyan and Tanzanian rift date to the early Pliocene. By ~5 Ma, the Aberdare volcanic complex had risen to > 4,000 m, thus forming a substantial orographic barrier in Kenya. This graben was broken apart 2.6 Ma in the central Kenyan rift and created the Kinangop Plateau, which harbours a tectonically active 40 km-wide inner rift. The rift shoulders we see today were formed 1.2 Ma and further influence local climatic conditions.

Carbon isotope records from soil carbonates and biomarkers (*n*-alkanes) taken from sedimentary records show that there was a gradual shift from C_3 to C_4 vegetation during the Plio-Pleistocene globally. This shift can be linked directly to aridification brought on by rifting in East Africa. C_4 photosynthesis demands less water than C_3 metabolism, leading to selection for metabolic systems that enhance survival in drier habitats.

6.4 The co-evolution of primates and humans in Africa

The initial divergence of the hominin lineage is likely to have taken place in West-Central Africa, in response to the mid- to late Miocene aridification between 10 and 7 Ma. The presence of *Sahelanthropus tchadensis* in 7 Ma old deposits in Chad, Central Africa, supports this prediction to some extent, whether the fossil respresents a common *Pan-Homo* ancestor, an ancestral hominin, or a previously unknown Miocene ape. The *Gorilla* lineage had already embarked on its own independent evolution 10 Ma, and remained in the West-Central African forests. Chad is likely to have been covered by forests and woodlands, if somewhat drier than those occupied by gorillas. Early hominins (4.0 to 2.0 Ma) occupied forested environments (Rayner et al. 1993), where they practised a unique form of locomotion that made them adept at both tree climbing and a form of bipedalism, possibly walking on the sides of their feet, as apes tend to do, rather than on the full plantar surface (Tattersall and Schwartz 2000). The genus *Paranthropus*, the “robust australopiths”, emerged around 2.7 Ma, clearly adapted to a highly fibrous diet that needed a great deal of processing, explaining their huge mandibles and cheek teeth, with a concomitant reduction in the size of the anterior teeth (Tattersall and Schwartz 2000; de Menocal 2004; Lee-Thorpe 2010). The Pliocene-Pleistocene transition 2.5 to 2.3 Ma saw the continued spread of C_4 grasslands (Bobe et al. 2006; Lee-Thorpe 2010) and the emergence of *Papio*, the savanna baboons. Grassland expansion is often associated with faunal turnovers, which links it not only to the emergence of *Homo*, but also to pulses of extinction and radiation of other mammal lineages (de Menocal 2004). The earliest stone tools are dated between 2.4 and 2.6 Ma, which has led to the assumption that only *Homo* was a toolmaker, although *Paranthropus* is also a potential candidate (Susman 1988).

As the environment shifted to more varied habitats composed of savanna grasslands, bushveld and woodlands, obligately bipedal hominins emerged ~1.8 Ma, and evolved the postcranial skeletal proportions present in modern humans. When *H. erectus/ergaster* first appeared in the Omo region, it was contemporaneous with grassland mammal fossils, indicating that the environment was less wooded by 1.8 Ma (Bobe 2006, Lee-Thorpe 2010). Shortly after bipedalism became established, *Homo* migrated to South-east Asia by way of what is now eastern Europe (Tattersall and Schwartz 2000). East African bovids from 1.7 Ma were adapted to arid environments (de Menocal 2004).

Just as climate change influenced biological evolution among primates, it may have affected the behaviour of hominins. Middle Stone Age (MSA) tools have been found at archaeological sites in Africa, including both weapons and digging tools. Some were comprised of rocks not found in the surrounding areas, indicating that they had been carried by the tool makers. The Olorgasaile formation, which covers a sedimentation time frame from 700 to 499 ka, is an Acheulean site that contains many stone tools as well as evidence of the use of pigments. The tools were preserved in aggrading lacustrine floodplains with low energy channels, and palaeosols that represent stable depositional conditions over this period.

The mammalian fauna associated with the Olorgasaile basin aslo indicates local mammal extinctions, including *Equus oldowayensis, Palaeoloxodon recki* and the extinct gelada baboon, *Theropithecus oswaldi*. These taxa were replaced by smaller-bodied mammals like *Antidorcas marsupialis*, the springbok, which covered a range > 2800 km^2, as it is also known from the archaeological site at Florisbad, South Africa. This supports the view that eastern Africa's dynamic environmental history was a major driver of turnover events, leading to local extinctions and recolonisation from southern African sources. Migrations between southern and eastern Africa are also indicated by the evolutionary history of *Papio* and *Australopithecus*.

CHAPTER SEVEN: SUMMARY AND CONCLUSION

This study compared patterns of evolutionary radiation in five clades of African primates that took place over different time frames between the Eocene and the Holocene (56 Ma to 10,000 years ago), in order to explore potential links between major events in primate (including human) evolution in Africa, and the tectonic evolution of the continent itself. I first characterised the pattern and timing of recently published phylogenetic trees for the following clades: (a) Lorisoidea (galagos and pottos); (b) arboreal guenon monkeys (Genus *Cercopithecus* and its allies); (c) the living African apes (including humans); (d) Papionini (baboons); and (e) savanna or “vervet” monkeys (Genus *Chlorocebus*). Where possible, I compared the results obtained from mitochondrial DNA (mtDNA) sequences with those based on nuclear DNA (nDNA). First, the mutation rate of mtDNA is more rapid than that of nDNA, which can lead to artificially ancient divergence age estimates. Second, the fact that mtDNA is largely maternally inherited, rather than being passed on by both parents, means mtDNA tree topologies are particularly susceptible to hybridisation events. Hybridisation between distinct species is always rare, but has been observed at relatively high frequencies between some primate species, particularly within the genera *Cercopithecus, Chloropithecus* and *Papio*. A close relationship between lineages revealed by mtDNA may hence be the result of hybridisation rather than evidence of common ancestory (Detwiler et al. 2005).

I then compared the major divergence age estimates among the African non-human primate clades with the dates of geotectonic events that transformed the evolving African landscape, as well as with broad patterns of climatic change and the consequences that such changes had for patterns and types of vegetation. Based on the current distributions of the descendant species in each of these clades, I then estimated the most likely geographic localities of the major divergence events. Finally, I compared the evolutionary patterns evinced by the molecular phylogenies of the non-human primate clades with hominin evolutionary scenarios. Unlike most non-human primates, the tribe Hominini is represented by a sole surviving species. Hominin fossils are fragmentary and sparsely distributed. My final aim was, therefore, to investigate whether a comparison of divergence times estimated from hominin fossils with those calculated for other primate lineages evolving alongside them could provide insights into the drivers of human evolution.

My study showed that primate evolution in Africa occurred under varying climatic regimes and the long-term tectonic activities of the EARS throughout the Cenozoic Epoch. These forces drove different patterns of diversification across the clades I examined. The mid to late Miocene period of general aridification took place over at least 10 Ma, while the EARS was propagating southwards. The papionins and cercopithecins began to adapt to different kinds of drier habitats, isolated in part as a result of tectonic uplift. The formerly continuous rain forests of West-Central Africa fragmented, coalesced, then fragmented again, and arboreal genera (bushbabies, pottos and arboreal guenons) diverged. During the Plio-Pleistcene, oscillations between humid and arid climatic phases, and consequent shifts from mesic to xerophytic vegetation, were extraordinarily rapid relative to the amount of time required for adaptation and speciation. This oscillating climate would have imposed contrasting forces of selection that changed direction rapidly and repeatedly, causing extinctions and, in rare cases, speciation. Vervet monkeys, baboons and humans evolved into the emerging drier environments. I consider this information as good evidence that there is a causal relationship among tectonism, climate and lineage divergence. Tectonic events, climatic changes and palaeovegetational shifts are intimately connected, and have synergistic effects on biotic diversity. Additionally, tectonic uplift and erosion would have imposed geographic barriers to movement by primates across the continent, increasing the likelihood of geographic and reproductive isolation of emerging taxa, and speciation. Hominins became adept tool makers, and evolved a method of locomotion that allowed them to travel long distances in search of food. The learned to control fire, and expanded their range across half the world.

Two questions arose out of my comparative study as distinguishing hominin evolution from that of other primates. First, our fossil lineage reaching back 7 Ma includes ~20 recognised species, but only one survives. In all the other extant clades, at least two species still persist. Why did none of these ± 19 lineages survive? Second, hybridisation is a relatively common feature of recently emerged species in *Cercopithecus, Chlorocebus* and *Papio*. Could some of the fossil variants recognised as species reflect hybridisation events? Despite these differences, we owe our emergence as a species to the same tectonic, climatic and genetic processes that led to the evolution of our primate relatives.

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