HUMAN ORIGINS, DISPERSAL AND ASSOCIATED ENVIRONMENTS: AN AFRICAN PERSPECTIVE

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Summary

Africa’s position as the cradle of humanity is widely accepted, supported by rich fossil and archaeological discoveries from different parts of the continent. Drawing on the Out-of-Africa theory of human origins, this article provides a condensed narrative of the major milestones in human evolution and associated environmental settings. The underlying hypothesis is that changes in global climate played an important role in fueling early modern human origins and dispersals within and outside of Africa. As one will discover in this article, the history of humanity is a tale of small events that merged together into major milestones over a long span of time. There is an emerging consensus among scholars that the onset of variable global climate throughout the last 6 million years, particularly the repeated glacial and interglacial cycles in the last 2.5 million years, drove the evolution of the biological and behavioral traits that define the human lineage. As with our past, the futurity of humanity will likely hinge on future climate patterns.

1. Introduction

The question of human origins has remained at the center of philosophical and scientific curiosities for centuries. The core issues surrounding current research on human origins revolve around two major questions: a) when exactly did the human lineage appear, possessing its distinct modern cultural and biological traits; b) where- in which geographic region did humans first appear? The question whether the human lineage emerged in one place or in multiple regions of the world has been at the center of anthropological discussions since the inception of the *Theory of Evolution* in the 19th century (Darwin, 1859). For a long time, Europe was considered the birthplace of the "superior human race" as it was there that ancient civilizations were believed to have first started (now we know that human civilizations began in ancient Mesopotamia and Egypt, both located outside of Europe). This belief was at the backdrop of Europeans' mindset when they imposed slavery and colonial ruling over many indigenous peoples.

Currently, there are two competing theories regarding the geographic origins of humanity, namely the Out-of-Africa and Multiregional models. The Out-of-Africa theory posits that early modern humans first appeared in Africa between 200 and 150 kya, and subsequently dispersed to the rest of the world replacing preexisting archaic humans in each region (Stringer and McKie, 1996; Oppenheimer, 2004). The Multiregional theory (Thorne and Wolpoff, 1992; WolPoff et al., 1994) maintains that modern humans appeared simultaneously in separate regions from an ancestral **hominin** that originated in Africa, and later dispersed to Asia and Europe sometime between 1.8 and 1.0 Mya. There are some scholars who support the Out-of-Africa model, but they advocate for assimilation and admixture between African and Asian *Homo sapiens* (Eswaran et al., 2005). By and large, the current debate on human origins remains firmly centered on Africa.

Drawing on the Out-of-Africa theory of human origins, this article provides a condensed narrative of the major milestones in human evolution and associated environmental conditions. The underlying theoretical baseline is that, different climatic episodes prevailed during the evolution of our lineage, and that changes in global climate played an important role in fueling early modern human origins and dispersals within and outside of Africa (eg., Finlayson, 2005).

2. The African Record

2.1. Background

Africa was long known as the "Dark Continent," but in the words of historians Paul Bohannan and Philip Curtin (1995), the darkness was in the ignorance of the outside world, not in Africa. Charles Darwin was among the first thinkers to label Africa as the likely cradle of humanity. In one of his seminal books, *The Descent of Man* (1871), Darwin made the following remark about the geographic roots of our lineage:

> "In each great region of the world the living mammals are closely related to the extinct species of the same region. It is therefore probably that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee; and as these two species are now man's nearest allies, it is somewhat more probable that our early progenitors lived on the African continent than elsewhere" (p.191).

By this statement, Darwin had foreshadowed important realities about the roots of humanity. A noteworthy insight was that humans are a single species that descended from an ape ancestor. This claim has been firmly established in the last century after genetic studies have revealed that humans and the African great apes are genetically close relatives (example: chimpanzees and humans are about 98% genetically similar). In Darwin's time, not much was known about genetics, and only a couple of hominin fossils had been identified, but his ingenious predictions had laid the foundations of our current views about human origins and diversity. Nowadays, Africa's place as the cradle of humanity is widely accepted, supported by archaeological and fossil discoveries from various parts of the continent.

2.2. Fossil and Archaeological Perspectives

Some of the leading fossil discoveries that placed Africa at the center of human evolutionary research have come from eastern, southern and central parts of the continent. Fossil remains belonging to one of the earliest hominin lineages, collectively known as the Australopithecines, were first reported from South Africa in the 1920s (Dart 1925). Soon after, East Africa became the focus of intensive research on human prehistory, resulting in the discovery of numerous famous fossil hominins and the oldest stone tools. Amongst the many fossils identified are the following: the famous fossil known as *Australopithecus afarensis* or Lucy (~3.3 Mya), *Ardipithecus ramidus* or Ardi (4.4 Mya), *Australopithecus anamensis (*4.2 Mya), *Australopithecus boisei* or Zinj (2.3 Mya) and *Orrorin tugenensis* dated to ~6 Mya (Johanson and Edgar, 1996; Klein, 2009; White et al., 2009b). More recently, the world's oldest hominin fossil named *Sahelanthropus tchadensis* or Tumai has been discovered in the Chad region of central Africa (Brunet et al., 2002). Dated to 6–7 Mya, Tumai exhibits a flat cranial base, suggesting a tendency toward upright posture. Thus far, discoveries of such antiquity have only been made in Africa (Figure 1).

Since the 1960s, Africa has seen important fossil discoveries related to the genus *Homo.* The emergence of the genus *Homo* sometime between 2.5 and 2 Mya was an important chapter in human evolution, because most hominins that appeared prior to this time were more apes than humans in their overall characteristics. It was with the appearance of the genus *Homo* that the human line started to achieve major evolutionary changes toward the modern condition, such as expansion of the brain, superior cognition, and technological innovations, to name a few. Traditionally, the genus *Homo* is divided into three successive species, namely *Homo habilis*, *Homo erectus* and *Homo sapiens,* with two other loosely defined variants (*Homo heidelbergensis* and *Homo neanderthalensis*) placed between the latter two (Klein, 2009). The oldest member of the genus *Homo*, *H. habilis,* is believed to have evolved between 2.5 and 2 Mya in the Turkana Basin (northern Kenya) and Olduvai Gorge (Tanzania) regions of eastern Africa (Wood, 1987), at about the same time as the emergence of tool-making behavior (discussed below). Colloquially referred to as the "handy man", *H. habilis* is regarded as one of the potential hominins responsible for making the first stone tools. Around 1.9 Mya, not long after the appearance of *H. habilis, H. erectus* with its definitive human-like anatomy and behavior emerged in Africa, and subsequently dispersed to Asia, where its remains have been discovered in southwest Asia and as far as China and Indonesia (Rightmire, 1993). Whether *H. erectus* directly evolved to *H. sapiens* or if other intermediate species existed between the two remains a contested topic. However, there is little contention about *H. erectus'* contribution to the human lineage.

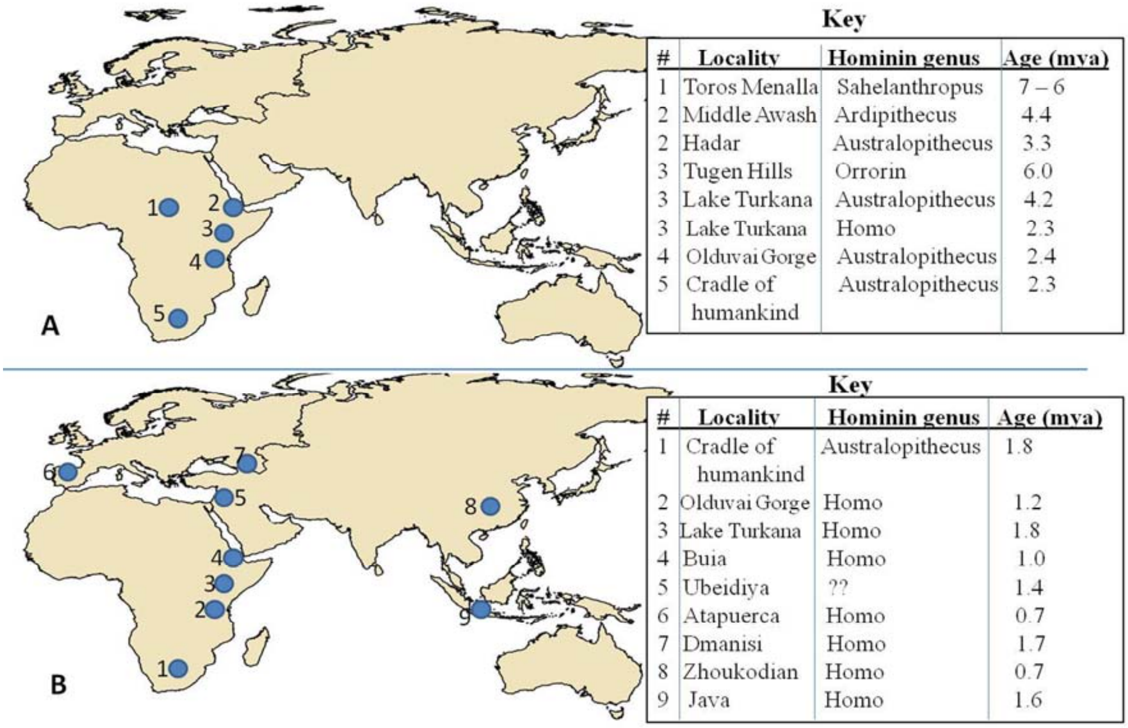

Figure 1. Map showing representative hominin fossil localities older than 0.5 Mya: A) hominin localities in Africa older than 2.0 Mya, B) hominin localities in Africa and Eurasia dating between 2.0 and 0.5 Mya. Note that all sites older than 2.0 Mya are found in Africa. Site information: Klein, 2009, Figures 4.4–4.6, 5.5, Table 4.7, and references therein. Map template source: ESRI © worlddata, drawn by A. Beyin.

The world's oldest *Homo sapiens* fossil remains have come from two sites in Ethiopia, namely Omo Kibish and Herto, dating to ~ 195 kya and 160 kya respectively (Leakey, 1969; White et al., 2003; McDougall et al., 2005). Tanzania, Kenya, South Africa and the Nile Valley have yielded equally important cultural and fossil evidence belonging to early modern humans, demonstrating that *H. sapiens* occupied a wider geographic range within the continent. According to the Out-of-Africa origin theory, members of the genus *Homo* had already settled in Asia and Europe prior to 200 kya, but only the African "archaic" *H. sapiens*, possibly populations represented by the Omo Kibish and Herto specimens, are believed to have evolved into modern humans.

Africa is also regarded as the birthplace of human culture. So far the oldest intentionally made stone tools have been recorded at East African sites, such as Gona (2.5 Mya, Ethiopia), Lokosalie (2.4 Mya, Kenya) and Olduvai Gorge (1.8 Mya, Tanzania) to name a few (Leakey, 1975; Semaw et al., 1997; Delagnes and Roche, 2005).Generally, most sites that date to younger than 2.5 Mya in Africa contain stone tool assemblages, making stone tool technology the longest-lived cultural innovation. Among other things, the oldest assemblages from African sites show evidence of sequential-decision making, involving selection of high quality raw material and employing consistent methods of flake removal from the original nodule (Delagnes and Roche, 2005; Barham and Mitchell, 2008). All these seemingly simple chains of events are thought to have involved changes in the hand morphology (to allow power and precision grip), planning, and social communities that can facilitate retention and transmission of technical skills. The overall pattern in the development of stone technology is that general purpose tools, referred to as choppers and handaxes, persisted for more than 2.0 million years after the initial appearance of tool-making behavior around 2.5 Mya (Barham and Mitchell, 2008). After 500 kya, specialized tools, such as projectile points and composite tools entered the human cultural spectrum.

2.3. Genetic Perspectives

In the second half of the 20th century, a significant number of anthropologists turned their attention to molecular genetics (**DNA** sequence) to resolve outstanding issues concerning the geographic and temporal origins of humanity. The leading assumption is that genetic similarities between species are due to shared descent. As such, species that share a recent common ancestor are expected to display greater genetic similarity than those that are more distantly related. Interestingly enough, the genetic make-ups of modern humans and that of the African great apes, specifically chimpanzees and bonobos, display about 98% similarity. On the basis of this figure, the date for hominin-chimpanzee split from the common ancestor is estimated between 8 and 6 Mya (Langergrabera et al., 2012). This finding has corroborated what Darwin had posited a century ago, when he stated that "it is somewhat more probable that our early progenitors lived on the African continent than elsewhere" (Darwin, 1871:191).

In recent years, mitochondrial deoxyribonucleic acid (mtDNA) has been a particularly useful tool for addressing important questions about human origins and prehistoric migrations (Forster, 2004; Pakendorf and Stoneking, 2005). Mitochondria are small organelles found inside the cytoplasm of the cell, but are located outside of the nucleus. They are responsible for supplying the cell with energy, and they have their own DNA primarily inherited from the mother. In the sperm they are stored in the tail; however, the tail (along with its mtDNA) is quickly destroyed upon entering the egg during fertilization. The mode of inheritance makes mtDNA suitable for reconstructing human genealogy along the maternal line. According to the current mtDNA data, the ancestral "Mother" to all modern humans appeared first in Africa sometime between 200 and 150 kya, and that African populations display greater genetic diversity implying that Africa was populated by human ancestors longer than any other region (Cann, 1988). Among other things, the genetic data has reinforced the Out-of-Africa origin theory and set possible scenarios for human dispersals out of Africa. Moreover, comparison of intra-population (within population) genetic diversity between modern humans and the great apes has shown that modern humans display lower intra-population genetic variability than the great apes, suggesting that all modern humans share a recently evolved ancestral DNA.

The main story anthropologists have so far put together using the genetic data is that, sometime between 80 and 65 kya, a genetically distinct human lineage carrying a mtDNA **haplotype** known as L3 migrated from east Africa into Arabia via the southern Red Sea. Soon after, descendants of this population launched northward and eastward dispersals from the Arabian Peninsula (Forster, 2004; Forster and Matsumura, 2005; Macaulay et al., 2005). This means that all contemporary non-African humans have descended from one African lineage (represented by haplogroup L3), which later split into two founding lineages known as M and N haplogroups (see Figure 5C). The age of haplogroup L3 is estimated to be ~ 85 kya and that of haplogroups M and N ~ 63 kya (Macaulay et al., 2005; Torroni et al., 2006). The two descendant haplogroups have somewhat distinct geographic distribution with the M lineages mainly concentrated in eastern African, South Arabian, Indian, and southeast Asian populations, whereas descendants of haplogroup N are mainly found in western and central Eurasia (Forster, 2004; Cabrera et al., 2009). The fact that there exists a close genetic similarity among human groups occupying different regions of the world today suggests that we all share a recent common ancestor. This means *Homo sapiens* is a young species by evolutionary standards.

3. Environmental Framework for the Origins of Humanity

As the sole foundation of life supporting systems, the natural environment (climate, landscape and associated biomass) represents an ideal context for assessing the forces that spurred human evolution and diversity. Since the publication of Charles Darwin's legendary volume, "*The Origin of Species by Means of Natural Selection*" (1859), there has been a growing recognition of the close links between the process of species evolution, and global environmental and climatic changes. At the center of Darwin's theory lies the notion that "**Natural Selection**" enhances the survival of those species that are able to adapt to their habitats, by virtue of possessing favorable traits. The history of humanity is about those moments when our ancestors acquired decisive traits that enabled them to successfully adapt to diverse environmental conditions to which they were exposed at different times and places.

Looking at how the earth's landmasses are distributed with respect to the equator, one can discern that there is more dry-land in the northern hemisphere than the southern hemisphere (Figure 2). This means that, for terrestrial species, such as humans, the northern hemisphere offers more available habitats. However, since a large part of the northern hemisphere's landmass also lies in the temperate and polar zones, the region is sensitive to variation in solar radiation.

At times when the earth was receiving low solar radiation, extreme cold and dry conditions would prevail across most regions that lie farther north of the equator, causing terrestrial species there to become extinct or be replaced by cold tolerant species. This happened more frequently in the past 2.5 million years due to long term fluctuations in the earth's orbit between circular to elliptical forms, affecting the amount of solar radiation received by the earth. The tropical regions, which account for about 75% of the African landmass, would have been less subject to extreme climatic fluctuations. Therefore, at times when the global climate was growing cooler and drier, habitats that lie within the tropical zone would have remained the most favorable/tolerable for terrestrial species, such as primates. It is for this reason that Africa is regarded as the likely place where our ape ancestors gradually evolved to modern human form without any major evolutionary gaps. In Eurasia (Europe and Asia together), the great apes and by extension hominins were likely subjected to multiple extinction events due to repeated cycles of cold episodes.

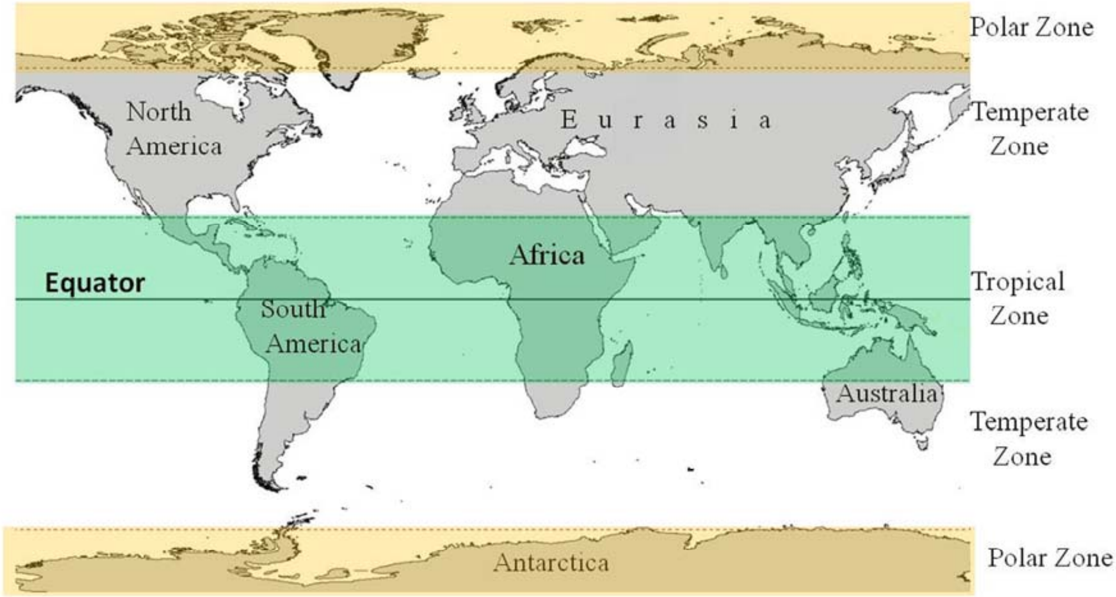

Figure 2. Map showing the major climate zones of the earth and landmass distribution with respect tothe equator. Note that the majority of the earth's landmasses lie north of the Equator. Regions most favorable for human life are found within the tropical zone, and this region saw the longest record of human settlement. Map template source: ESRI © worlddata, drawn by A. Beyin.

One may rightly ask, under what conditions did the defining characteristics of humanity evolve? At the present, there are two major hypotheses regarding the habitats that fostered the path to humanity, namely the "savanna hypothesis" (Laporte and Zihlman, 1983; Vrba et al., 1989) and the "variability selection hypothesis" (Potts, 1998). According to the savanna hypothesis, increased aridity and the emergence of savanna landscapes toward the end of the Miocene epoch (6 - 5 Mya) created a new survival dilemma for forest adapted apes. The dominant plants in the savanna are grasses, which are not readily edible by primates. To offset this dilemma, some primates may have switched to foraging on the ground. Under such a circumstance, bipedal walking may have emerged as an effective adaptation for energy conservation while foraging on the ground. Because only two limbs are engaged during bipedal locomotion, it costs less energy to walk on two limbs than on four.

The "variability selection" hypothesis emphasizes on the potential role of environmental instability in fostering the evolution of those characteristics unique to humans, such as bipedal walking, large brain and tool-making behavior. The underlying assumption is that environmental fluctuations in the last 6 million years compelled hominins to develop behaviors and anatomical structures responsive to varied habitat types (Potts and Sloan, 2010). In view of that, the expansion and contraction of forests *vis-a-vis* grasslands are thought to have stimulated the evolution of those crucial traits that lent humanity a decisive edge. One discovery of particular interest is a recently published 4.4 million years old hominin from Ethiopia called Ardi (White et al., 2009a). The local geology and associated fossils at the site suggest that Ardi lived in a predominantly forested habitat, thereby implying that grasslands may not have always been the primary environment where hominins thrived as is commonly perceived. For some time, a minority group of scholars have advocated for an aquatic origin of humanity (Morgan, 1982; Verhaegen, 2013). Dubbed the “Aquatic Ape Theory”, the proponents of this idea claim that the human lineage went through an aquatic stage during the transition from the last common ancestor we shared with other hominins, citing some anatomical features and behaviors believed to be present in humans and aquatic mammals only, such as loss of body hair, skin-bonded fat deposits, and ventro-ventral copulation. Currently, the theory remains largely ignored by mainstream anthropology for a lack of supporting **paleoenviornmental** and fossil data (Foley and Lahr, 2014).

Researchers utilize a wide-range of methods to reconstruct past climate and environments in an attempt to assess the potential effects of habitat variability to human evolution and survival. One of the well established approaches for reconstructing past climate changes involves analysis of oxygen **isotope** variation (^{16}O vs ^{18}O) from deep-sea cores (Shackleton, 1967). The underlying assumptions of this approach are that evaporated water is rich in the lighter oxygen isotope (^{16}O), and that during glacial times more evaporated water is trapped in the polar ice sheets, causing sea levels to drop several meters below their present height. This phenomenon leaves the ocean waters rich in the heavy oxygen isotope (^{18}O). Long columns of deep-sea sediments are cored, from which ocean-dwelling organisms called foraminifera are extracted. The oxygen isotope contents of the foraminifera are then examined, and the results are translated to global climate patterns. For example, oceanic foraminifera rich in ^{18}O would translate to cold conditions, because during such episodes the marine organisms will incorporate more of the heavy oxygen as the lighter isotope would remain trapped in the polar ice sheets. Conversely, oceanic foraminifera representing interglacial episodes (associated with warm conditions, accompanied by ice melting) contain higher proportion of ^{16}O. Patterns of past climate changes have also been determined using terrestrial deposits and from proxy sources, such as lake deposits, analyses of dental and bone chemistry of animals that thrived in the past, and **palynology**. All of these methods are shedding new light on the environmental contexts that framed human evolution and dispersal.

Paleoenvironmental data derived from marine and terrestrial settings show that Africa had seen dramatic fluctuations in climate in the past 3 million years, compelling hominins to be adaptive and competitive (Barham and Mitchell, 2008). Successive cycles of glaciation and deglaciation prevailed throughout most of the Pleistocene epoch (2.5 Mya - 12 kya). Some of the climatic pulses were abrupt, others occurred after long intervals. Prior to 0.9 Mya, the glacial cycles lasted for shorter periods (~ 40,000 years). Whereas after 0.9 Mya, the glacial intervals lasted much longer (about 120,000 years) while interglacial cycles were shorter in duration (Muller and MacDonald, 1997). Citing the paleoclimatic record of Africa (deMenocal, 1995), Barham and Mitchell (2008) mention rapid climatic changes at 2.8, 1.7 and 1.0 Mya. Repeated and intense ice ages hit the world in the subsequent periods, with the last one (the Last Glacial Maximum) dating between 25 and 22 kya. The potential effects of such repeated cycles of glacial and interglacial episodes may have included the contraction and expansion of habitats suitable for hominin adaptation.

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