Origins of Hominin Biocultural Diversity

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„Reclaiming African history enables a reconnection to humanity“
(Jacques Depelchin, 2010)

Since 1921 fossilized hominin remains have been recovered in Africa. Initially, the proposition that these were human ancestors was met with ignorance, as this conclusion conflicted with a predominant eurocentric scientific world view. Today, after numerous further finds in southern, eastern, northeastern, and central Africa, it is unequivocally accepted that the cradle of both earliest hominins and earliest humans lay in Africa. Convincing evidence shows that environmental and biogeographic variability triggered profound evolutionary changes such as the beginning of upright walking (8-6 Ma) and the onset of cultural evolution between 3 and 2.5 Ma, which are the two most crucial stages of early hominin evolution. A large body of evidence to date, including palaeontological, geological, environmental, archaeological, ecological and biogeographic data allow the reconstruction of the major phases of early hominin evolution, including the onset of biocultural evolution of humans in Africa. This review is dedicated to Peter Breunig, in recognition of his interests in the interactions of culture and nature as well as in the history of Africa.

KEY WORDS: African history, early hominins, biocultural evolution, biogeography

Introduction

Since the 1920’s, fossil hominins have been unearthed in Southern Africa and in Eastern Africa since the 1950’s. Initially, the proposition that these were human ancestors was met with rejection and ignorance. Since the time of Herodot, the European view was that Africa had no proper history because written documentation alone was the standard of historiography, and oral transmission of history common in many African societies did not correspond to this norm. Especially for Europeans, no other place of origin of mankind was conceivable than Europe. Fortunately, however, today a very broad range of sources – e.g. fossils, artefacts, genetic analyses, environmental and geoliogical data – are accepted and utilized in historical research. After numerous finds of fossil hominin remains in Southern, Eastern and Western Africa, it is today unequivocally accepted that the cradle of earliest hominins and of early Homo lay in Africa. Early hominin fossils have been found at an ever increasing rate during the last decade owing to great public interest in tracing the origins of modern humans existing as fossils in Africa today.

Fossil Evidence

The first African hominin remains were found in Zimbabwe, 1921 (Woodward 1921), and in 1924 in South Africa (Dart 1925). Thousands of hominin fragments have now been discovered at more than 50 African sites (Fig. 1), comprising roughly 10 genera and 20 species. The majority of specimens originate from South African cave fillings. Probably the oldest hominin species found so far, Sahelanthropus tchadensis, is from the Chad Basin (~ 7 Ma; Brunet et al. 2002) (Fig. 1), and broadly indicates the time of chimpanzee-hominin divergence esti-
mated at 8-6 Ma (Langergarber et al. 2012). *Orrorin tugenensis* from the Kenya Rift (6-5.7 Ma; Senut et al. 2001) and *Ardipithecus kadabba* (5.8-5.2 Ma; Haile-Selassie 2001) from the Afar add to the list of late Miocene hominins. The oldest (4.4 Ma) Pliocene hominin is *Ardipithecus ramidus* also from the Afar (White et al. 2009).

Most of the more recent Pliocene hominins from ~ 4.2 Ma onwards, whose attribution to the hominin lineage is unambiguous, belong to the genus *Australopithecus* and derive mainly from the Eastern Branch of the East African Rift System (EARS) and Southern Africa (Wood & Lonergan 2008), with the exception of *Australopithecus babreghazali* (Brunet et al. 1995) from northern Chad, and fossils of *Australopithecus afarensis* from Kantis (near Nairobi) to the east of the EARS (Mbua et al. 2016). The youngest Pliocene hominin fossil at 2.8-2.75 Ma is from the northern Ethiopian Rift that to date represents the earliest appearance of the genus *Homo* (Villamoare et al. 2015), slightly pre-dating early *Homo* from the Northern Malawi Rift at 2.6-2.4 Ma (Schrenk et al. 1993).

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

### Hominin fossils and their Environment

Hominin fossils are exceedingly rare in the geological record. Therefore, detailed aspects of their evolution, as reflected in patterns of distribution and diversification, are not well resolved. All but a very few hominin fossils are from the Eastern Branch of the African Rift (Bonnefille 2010). The Western Branch of the African Rift have yielded hominins in only the northern part of the Malawi Rift (Schrenk et al. 1993) and the Albertine Rift (Crevecoeur et al. 2014) (Fig. 1). Overall, widespread lake formation led to increased environmental diversity, which potentially influenced the evolution of hominins by altering their habitats. Having said this, however, the discovery of abundant fossils in the African Rift might represent a taphonomic bias, as it is mostly in the rift basin badlands where reasonable potential for preservation and discovery of hominin fossils exists (Ring 2014).

A challenging problem in hominin research is to relate global and regional climate changes to shifts in palaeoenvironments and species occurrences, dispersal and evolution (Behrensmeyer 2006; Potts 2007; Levin 2015). Climatic and environmental factors that drove the chimpanzee/hominin split and the subsequent evolution of hominins remain poorly known. It is often argued, that climate changes causing a transformation from tropical forest to savanna-type habitats (*i.e.*, a change from C4 to C3 environments) were the main drivers of early hominin evolution. A review of Cenozoic vegetation and climate by Bonnefille (2010) concluded that an expansion of savanna/grassland at ~10 Ma in East Africa took place after the 15.5-12.5 Ma cooling event. Another pronounced change in vegetation took place at 6.3-6.0 Ma and was marked by a decrease in tree cover across all of tropical Africa. Thus, the major evolutionary transition to hominins at this time most likely occurred in early wooded savanna ecosystems that were increasing at the expense of diminishing African rainforest towards the end of the Miocene (Schrenk et al. 2004).

Vertebrate faunas provide important evidence for the ecological context of hominin evolution over a wide range of scales, from site-specific analysis of taxa directly associated with hominin fossils, to faunal trends indicating long-term environmental change that could have affected human evolution (Behrensmeyer et al. 2007; Macho 2013; Potts 2013). The earliest hominins found in the Kenyan and Ethiopian Rifts and in Chad, inhabited mixed C3/C4 environments, comprising grassland with patches of woodland (Cerling 1992). *Ardipithecus kadabba* in Ethiopia lived in riparian woodland and floodplain grassland along water margins (Su 2014). WoldeGabriel et al. (1994) argue, that after 4.4 Ma hominins started to inhabit environments with more open vegetation. These interpretations of the habitats of the African late Miocene and early Pliocene suggest that the beginnings of our lineage occurred in rather closed and/or wet habitats.

The evolution of the genus *Homo* in the early Pleistocene can only be understood by integrating palaeontological, geological, archaeological and environmental data on seasonal, intergenerational and evolutionary time scales. Hypotheses that have been put forward to explain and test processes of selection and speciation in
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Plio-Pleistocene hominin evolution include the Turnover Pulse hypothesis (Vrba 1999) and the Pulsed Climate Variability hypothesis (Maslin et al. 2015). The Variability Selection hypothesis (Potts 2007, 2013), the most comprehensive approach to early hominin evolutionary patterns to date, refers to adaptive change in response to environmental variation.

Early *Homo*

The search for the roots of the genus *Homo* is of particular interest in the field of paleoanthropology, since the determination of the earliest putative *Homo* fossils provides the basis for the definition of the taxon *Homo*, to which all modern humans belong. Carolus Linnaeus established the genus *Homo* in the tenth revision of his “Systema Naturae” in 1758, with *Homo sapiens* comprising four geographical variants from Africa, America,
Asia and Europe. In the two centuries to follow, *Homo neanderthalensis* (King 1864), *Homo heidelbergensis* (Schoetensack 1908), *Homo erectus* (Dubois 1892; Mayr 1944), *Homo habilis* (Leakey et al. 1964), *Homo ergaster* (Groves & Mazák 1975), *Homo rudolfensis* (Alexeev 1986), *Homo antecessor* ( Bermúdez de Castro et al. 1997) and others were included in the genus. The history of research, their order of discovery, as well as a variety of paradigms heavily influence interpretations of human evolution. This holds true especially for our understanding of the origin of the genus *Homo* since the 1960s. Debates on the attribution of fossil specimens and the definition of the genus continue up to today.

One of the hallmarks of early *Homo* is an increased brain size, which was larger than that of the *Australopithecus*, but smaller than later *Homo erectus*. Endocasts of *Homo habilis* from Olduvai and Koobi Fora reveal a number of distinctive features, some of which are recognized as autapomorphies of the genus *Homo*. Tobias (1987) underlined the principal morphological trait that distinguishes *Homo habilis* from *Australopithecus* by a larger mean endocranial capacity in the former (640 cm³) than in *Australopithecus africanus* (441 cm³), *Australopithecus boisei* (513 cm³) and *Australopithecus robustus* (530 cm³). This suggests that the evolutionary trend towards the extension of the brain was already well under way more than two million years ago. The *Homo habilis* mean (640 cm³) is close to the lower limit (647 cm³) of the 95% population range of *Homo erectus*, but well above the upper limit of the *Australopithecus africanus* range (492 cm³). The brain capacity of type specimen of *Homo rudolfensis* (ca. 700 cm³) (Bromage et al. 2008) is even larger than the known range of the *Homo habilis* specimens from Olduvai Gorge and Koobi Fora and falls within the lower range of *Homo erectus*.

A prominent feature of the *Homo habilis* brain is the bilateral transverse expansion of the cerebrum, especially of the frontal and parieto-occipital areas, and a heightening especially posteriorly. The increased bulk of frontal and parietal lobes of the cerebrum and the sulcal and gyral pattern of the lateral part of the frontal lobe have been interpreted as derived features in the genus *Homo* (Tobias 1987). The *Homo habilis* brain probably showed well-developed superior parietal lobule, more on the left than on the right and a prominent development of the inferior parietal lobule, an autapomorphy of *Homo*.

The endocast of KNM-ER 1470 shows a sulcal pattern in the left frontal lobe that is associated with Broca’s speech area in living people (Falk 1987), a finding that has lead to the conclusion that *Homo rudolfensis* may have been capable of speech. This conclusion is in accordance with Holloway’s observation of a pronounced left-occipital-right-frontal petalial pattern in the endocast of KNM-ER-1470 that may indicate functional cortical asymmetry (Holloway 1983). Tobias (1991) stated that *Homo habilis* is the earliest hominin to show prominently enlarged Bocas’s and Wernicke’s areas, interpreted as the brain’s centre for speech capability. If so, the same should be addressed for *Homo rudolfensis*. *Australopithecus* endocasts show the Bocas’s area, but not the Wernicke’s region, while anthropoid apes display neither of these areas. The prominent, protuberant development of the two speech areas may thus be seen as an important autapomorphy of the genus *Homo* (Tobias 1991). Even if *Homo habilis* and *Homo rudolfensis* possessed the neurological basis of speech there is no evidence that one of them used spoken language. The areas on the brain that control spoken communication probably manifest themselves only with the start of marked encephalisation.

**Early Homo Biocultural Ecology**

During the late Pliocene at ~3.5 Ma, hominin diet, especially of *Kenyanthropus*, began to include higher amounts of C4 food resources (Cerling et al. 2011). By ~2.8 Ma, dryer conditions prevailed in the African landscape (Vrba 1999; deMenocal 2004). Lüdecke et al. (2016) highlight major differences in ecosystems between the Eastern Branch and the Malawi Rift in the Plio-Pleistocene indicating high behavioral flexibility of early hominins, triggered by abiotic changes (Bromage et al. 1995; Macho 2013).

Extensive open habitats with more arid-tolerant vegetation developed. The resulting selective pressures apparently led to increased survival of megadont varieties capable of feeding on tougher fruit and open woodland-open savanna food items. This is true for early hominins as well as numerous large eastern and southern terrestrial African vertebrate lineages at ~2.5 Ma (Turner & Wood 1993) and resulted in the phyletic splitting of *Australopithecus afarensis* into *Paranthropus* and *Homo* lineages after ~2.8 Ma (Bromage & Schrenk 1999; Strait et al. 2015).
This points towards an evolutionary alternative of the massive mastication system of *Paranthropus*, which was equally able to deal with hard food properties. This alternative was the manufacturing and use of stone tools. The earliest record of stone tools just postdates the end of the Pliocene warm period: Harmand et al. (2015) reported stone tools from Lake Turkana dated at 3.31-3.21 Ma, discovered in the same sediments where fossils of the hominin species *Kenyanthropus platyops* were found (Leakey et al. 2001). This is broadly coeval with animal bones from Ethiopia that bear stone-inflicted cut marks, dated to ~3.39 Ma (McPherron et al. 2010; Thompson et al. 2015).

At many sites the co-occurrence of more than one hominin species, found in the same horizons as early Oldowan pebbles, does not permit a clear evidence of who were the first tool makers. However, the distinct specialisation of the skull and dental morphology in robust australopithecines and the brain expansion in early *Homo* point to the latter as the most likely tool manufacturer. Implements are widely used by higher primates. Yet, during marked habitat changes which led to pronounced changes in food resources, it was the invention of culture, which led to the origin of the genus *Homo* around 2.5 Ma ago. Increasing independence from the environment led to an increase in the dependence on culture, a characteristic challenge for humans up to today.

If early *Homo* utilized stone tools to prepare food, the dentition might actually indicate these behavioural changes in food acquisition. However, the basic morphology of early *Homo* teeth does not seem to suggest an extensive food preparation before ingestion. The incisors are large compared to those of *Australopithecus* and *Homo erectus* and the canines are large relative to the premolar crown surfaces. The premolars are narrower than in *Australopithecus* and fall within the range of *Homo erectus*. Molar size overlaps the ranges for *Australopithecus* and *Homo erectus*. Especially the cheek teeth of *Homo rudolfensis* are enlarged and show affinities to *Paranthropus* molars.

In *Homo habilis* we see well-developed third molars, while in *Homo rudolfensis* the third molar forms a smaller crown than the second molar. The occlusal surface of the cheek teeth is not as broad as in australopithecine molars and indicates differences in chewing. Tobias (1987) mentioned that the relief of the crown’s cusps is still present, even when the teeth are in advanced wear and dentine is visible. This means that the attrition of enamel is less pronounced as in earlier hominin types. Differences in tooth wear between *Homo rudolfensis*, with megadont teeth and a more horizontal tooth abrasion, and *Homo habilis*, with its more gracile molars and a higher relief in worn teeth are visible. This indicates significant differences in diet and ecology of early *Homo* species.

*Homo rudolfensis* and the robust australopithecines share some cranial and dental features concerning the morphology of the masticatory apparatus (Wood 1992), which indicates that these hominins were able to cope with tough fruits and other plants in the African savannas. Since those features are judged as an adaptation to more dry climatic conditions, they also show that *Homo rudolfensis* was relatively conservative in the nutrition spectrum and probably largely followed an herbivorous strategy in food acquisition.

### Early Hominin Biogeography

The behavioural inclination of earliest hominins, distributed along the edge of the tropical rain forest was to maintain a connection to and to remain near the borders between broad riparian habitats and open woodlands during the ascendency of more warm and humid times. Over short geological time scales, this was typically a local, non-dispersing tendency, but by approximately 4.0 Ma several species of *Australopithecus* successfully dispersed throughout the reaches of the African Rift Valley and into Western Africa (Fig. 2). Over longer time frames this included dispersal through the riparian “corridor” connecting eastern and southern Africa permitting population dispersal into southern Africa by 3.0 Ma. This dispersing unit maintained habitat specificity’s to forested environments (Rayner et al. 1993), though in more environmentally temperate climes and in relative geographical isolation at the extreme distal edge of its distribution. The dispersion along changing latitudinal circumstances co-varied with the transformation of earliest hominins into, first, a geographic variant and, subsequently, into *Australopithecus africanus*, joining ranks with other southern African endemic faunas. Thus *Australopithecus aferensis* was essentially an eastern African endemic and it follows that no typical representatives are likely to be recovered from southern African deposits older than 3.5 Ma.
By approximately 2.8 Ma the initiation of cooler and dryer conditions prevailed upon the African landscape, its vegetation, and its faunas, until climaxing ca. 2.5 Ma (Bonnefille 2010; deMenocal 2004). During this time Australopithecus afarensis in eastern Africa and Australopithecus africanus in Southern Africa were each subject to unique palaeobiogeographic consequences of global cooling and aridification, in accordance with the Habitat Theory of Vrba (1999).

For Australopithecus afarensis, then, the changing climate meant vicariance of its habitat and its distribution into more removed ecotonal riparian and closed lake margin environs. During the interim between ca. 2.8 Ma and 2.5 Ma these changing conditions engendered more extensive open habitats comprising more resistant arid-tolerant vegetation around the remaining relatively lush but narrowed “ribbons” of tree-lined riverine forest. The selective pressures of this habitat change resulted in the increased survival of more megadont varieties capable of feeding on tougher fruit and open woodland-open savanna food items. This was so for early hominin as well as numerous eastern and southern African large terrestrial vertebrate lineages ca. 2.8 Ma (Turner & Wood 1993). These pressures were likewise sufficient to result in the phyletic splitting of Australopithecus afarensis into Paranthropus and Homo lineages by ca. 2.8 Ma (Bromage & Schrenk 1999).

Ensuing cooler and dryer conditions favoured a tougher savanna vegetation composed of plant species better able to retain their moisture under such conditions. Selection favoured more facially robust and large molar-toothed mammals, including early hominins, capable of efficiently processing the tougher, more durable, vegetation of the savanna. Selection pressures led to evolutionary splitting of Australopithecus afarensis into Paranthropus and Homo lineages by ca. 2.8 Ma. Our evidence suggests that the tropical equatorial animals, including the hominins, of eastern Africa stayed in the tropical African ecological domain, while during the drying and cooling of global climates ca. 2.8 Ma, the southern and more temperate African faunas followed their northward-drifting vegetation zones. Thus Homo and Paranthropus may have emerged in tropical Africa as a result of the ca. 2.8 Ma climatic cooling event and remained there.

The beginnings of the Paranthropus lineage maintained a reliance on fruiting resources on the riverine side of its ecotone, particularly during the dry season, but it was equally adept at grinding on the postcanine dentition those food items it required from more open habitats during more hospitable times of the year. The beginnings of the Homo lineage ca. 2.8 Ma, and also represented by Homo rudolfensis, was an endorsement of its recency of common ancestry with Australopithecus afarensis, a distinction it shared with Paranthropus (Bromage et al. 1995).

However, while Paranthropus was principally adapted by means of a robust masticatory system to its tough and abrasive diet, Homo rudolfensis exhibited an increased behavioural flexibility as its adaptation to climatic circumstances included a larger and more provoking, inquiring, and capable brain. This included a shift to proportionately less abrasive foodstuffs and more omnivorous habits. Material culture ameliorated the effects of climate change to the degree that it enabled Homo rudolfensis to take advantage of other resources more efficiently than was ever possible before. Paranthropus boisei and Homo rudolfensis remained endemic to tropical latitudes during this time (Bromage et al. 1995). The eastern African tropical faunas, having habitable alternatives, remained within their biogeographic domain rather than brave the relative deterioration and paucity of habitats south of the African Rift Valley.

The faunas of southern Africa were subject to a different set of environmental sequelae during the ca. 2.8 Ma cooling event. Waning of the forests and woodlands in deference to more open arid grasslands invigorated not only evolutionary adaptations to savanna life in tropical eastern Africa, but also resulted in the distribution drift northward of faunas tracking the equatorward shift of grassland and woodland biomes into eastern Africa from the south ca. 2.8 Ma (Bromage et al. 1995). The temperate zone ca. 2.8 Ma experienced more seasonal extremes, and many organisms unwittingly maintained their inherited preference for moderately seasonal climes and temperate vegetation physiognomy by moving northward with the shrinking of this biome toward the equator, effectively transgressing the Zambezi Ecozone. Amongst these migrants was Australopithecus africanus who, having been adapted to a modest temperate ecology, now found its suitable habitats shifted to the north toward the African Rift Valley. While dispersing toward the eastern African tropical domain, selection for increased behavioural flexibility was related to the habitat diversity of the tropics and the presence of other non-vegetative food resources available in their new region. This emerging taxon, Homo habilis, rapidly established itself as a categorical omnivore and found that it could buffer itself more resolutely from environmental changes. This enabled it to cross-habitat boundaries more easily and also to advantage itself of more resources with its material culture.

By approximately 2.0 Ma Africa was rebounding from its relatively cool and dry climate to return to slightly more warm and humid conditions (Bromage et al. 1995). A phase of biome expansion ensued that facili-
Fig. 2. Chronology of hominin evolution in relation to regional distribution of early hominins. (update Dec 2017, fs)
tated dispersions away from the equator, ending nearly one million years of relative endemism dominated by tropical equatorial speciations. *Paranthropus boisei* dispersed southward along re-established ecotonal habitats into southern Africa, varied there as a geographic variant under more temperate conditions, and evolved into *Paranthropus robustus* (Fig. 3). *Homo habilis* expanded southward into the southern African temperate domain but it maintained a very much broader niche and increased its distributional area as a single species. *Homo rudolfensis* remained endemic to the eastern African tropical domain due partly to its preference for more open habitats around the rain shadows of the African Rift Valley and partly, perhaps, to some small measure of competitive exclusion from geographic realms occupied by *Homo habilis*.

The onset of warmer and more humid conditions around 2.0 Ma finally favoured the first phase of human emigration out of Africa. Shortly afterwards hominins appeared in Western Asia (Dmanisi) (LORDKIPANIDZE ET AL. 2013), Southern Europe (Orce) and in South East Asia (Java). While it is likely that *Homo erectus* was the first taxon to spread into Asia and Europe, it is possible, that even *Homo floresiensis*, who survived until 18,000 years ago on the island of Flores, Indonesia (BROWN ET AL. 2005), is a direct descendent of the earliest hominins who left Africa around 2 Ma ago.
Reclaiming African History

Today Africa is considered to be the birthplace of pre-humans and earliest humans. Biologically modern humans also originated on the African continent about 160,000 years ago and populated most habitats of the earth from here. The evolution of *Homo sapiens* not only refers to a biological process, but to a rather complex history, characterized by long-term interdependent biological, cultural and social processes. Today, ideas and technology are widely considered to drive innovation, Africa was the seed of technology, the seed of innovation. In a very real sense, every piece of technology and ideas, can be traced back to the first tool ever crafted by an early hominin.

The geographic location of the origin of *Homo sapiens* was always highly controversial in science, as it was thought that the place of human origin would identify the birthplace of civilisation. Today the discussion is dominated by questions of identity and culture. Yet, with the “Out of Africa” concept, the identity-creating origin of *Homo sapiens* is attributed to a continent, which much of the rest of the world has denied capacity to develop. However, for the field of palaeoanthropology, the African continent is not only a research location, but a place for answering questions about the birth of humans – questions that ultimately are of great political relevance.

Interpretation of history by individuals and societies is determined by ideologies. This applies to the more recent history as well as to the biological evolution of humans and to prehistory. During the last few hundred years the arrogance of colonial heroes and their intellectual supporters has either denied the historical knowledge and the historical consciousness of the autochthonous population in Africa, or, with a few exceptions, reinvented their own rules relating to biological racism and cultural hierarchy: Africans were – apart from a few territories in the north and east of the continent – no bearers of history, but culturally and intellectually underdeveloped “indigenous peoples”.

This mindset, created in the early modern period and valid through to the 20th century, still has significant influence today. In modern times, the world has been divided into so-called developed and underdeveloped (or developing) countries. Developed countries were held as models for determining the development requirements of underdeveloped countries. In today’s scientific collaborations – including those in palaeoanthropology – mindset still manifests itself, not the least of which includes the granting access or not to resources.

The current foreclosure of prosperity regions prevents uniform living conditions for *Homo sapiens*. However, this will not be successful in the long term – for many generations – since only a global cultural network can secure the survival of modern people around the world, as has been shown by our long history.

The meaning of history for individuals and societies is a result of their culturally-filtered interpretation. This applies to modern history as well as to the biological and cultural history of humans. Our present knowledge in palaeoanthropology, therefore, offers the great opportunity to reconstruct the manifold, complex and interwoven historical processes that shape humankind, thus contributing to the reclaiming of African history for the African continent.

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