Human Evolution: Theory and Progress

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Human Evolution: Theory and Progress

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Introduction

In one of the most remarkable understatements in the history of science, Charles Darwin wrote about his theory of evolution by natural selection that "light will be thrown on the origin of man and his history" (Darwin 1859: 488). That was practically all Darwin was prepared to share about the consequences for humankind of his theory in the *Origin of Species*, the seminal work on modern evolutionary ideas. But everybody around him immediately understood the implications, and as archaeological evidence and human fossil remains accumulated during the nineteenth and twentieth centuries in combination with genetic data, theories of human origins eventually became the science of human evolution.

Often overlooked, but central to Darwin's original method and the force of his argument, is the power of converging evidence from a number of different disciplines and bodies of knowledge. For the general theory of evolution, these originally included geology, paleontology, zoology, botany, physiology, anatomy, and, famously, selective breeding. Similarly, human evolutionary studies today are characterized by their multidisciplinarity. Whereas archaeology and paleoanthropology have been central to defining early human history, pushing the chronological boundaries of the first of everything further back in time, they no longer stand in unique positions to the understanding of the evolutionary history of humans.

Definition

Every extinct and extant species on earth have resulted from the same evolutionary processes determining the way they are through shaping their morphology, physiology, and behavior. The traits specific for the human species are the result of the same evolutionary processes responsible for any other living creature. From a general evolutionary perspective, humans are consequently no different than any other species on the planet. Human evolution refers to the natural process involved in the evolutionary history of all members of the human clade (consisting of *Homo* and other members of the human tribe, *Hominini*, after the split from chimpanzees and bonobos). Members of the human clade are referred to as hominins. Previously, the date, nature, and identity of the last common ancestor between modern humans and their closest living relatives were determined on the basis of comparative anatomy of living species and fragmentary fossil remains. Today, molecular genetic data play an increasing role in establishing phylogenetic relatedness between hominoids, the superfamily including all living and extinct ape and human species. Theories of human evolution refers to the complex defining methods, practices, hypotheses, models, explanations, and interpretations of data, answering the question what makes us human from an evolutionary perspective.

Historical Background

Nineteenth-century discovery of early human archaeological and fossil remains led to a systematic investigation of human origins using a scientific explanatory framework. The gradual

acceptance of deep time that eventually included humans gave rise to the scholarly division of human history into history and prehistory. Deep history was connected to a deep evolutionary ancestry with the introduction of the scientific theory of descent with modification. A number of key events and publications were instrumental in shaping early theories of human evolution, including among others the publication of Darwin's *Origin of Species* (1859) and *Descent of Man* (1871), Charles Lyell's *Geological Evidences to the Antiquity of Man*, Thomas Henry Huxley's *Evidence as to Man's Place in Nature* (1863), and John Lubbock's *Pre-Historic Times* (1865), the discovery of Neanderthals in Gibraltar, Belgium, Germany, and France, along with archeological artifacts such as stone tools and kitchen midden remains from early settlements, and cultural expressions such as cave paintings found in Spain and France.

From the second half of the nineteenth century, theories of human evolution were largely driven by discoveries. Archeological evidence, which includes any objects that have been made by hominins, played an important part in generating evidence and establishing theories about the behavior of early modern humans. Comparative anatomy, which reasons that organisms that are closely related to each other share many anatomical similarities, was another source of knowledge establishing evolutionary kinship. But fossil evidence was generally seen as most important to prove evolutionary theory right, leading to a race to find the Missing Link connecting humans and apes (Reader 2011; Kjærgaard 2011).

With a limited fossil record, many questions in human evolution remained speculative. It was thus more a theoretical preference and indeed the order in which fossils were discovered at different locations that determined the favored geographic local of human origins. Darwin had tentatively suggested Africa, but he was a minority. Asia was generally seen as the most likely place for the cradle of humankind, which was supported by Eugène Dubois' recognition of the first *Homo erectus* (1891–1892) found, at the time known as the Java Man echoing the location of the excavations. With a number of fossils turning up in Germany, France, Belgium, and Britain, including the first recognized Neanderthal (1856), *Homo heidelbergensis* (1907) and the notorious Piltdown Man (1912), Europe entered the race to find the first human. The discovery of *Australopithecus africanus* in South Africa 1924 was initially met by skepticism and the location of the true origin of humans remained undecided.

With the increasing number of early human fossils, in particular from Africa (Fig. 1), the resolution of the human family tree got better. But still with so few fossils to build ancestral phylogenies, there continued to be great difference in opinion among leading paleoanthropologists. Some argued for few species, others for a larger variety of early hominins. These groups are commonly referred to as lumpers and splitters. The scarcity of fossil data also made room for radically diverging interpretations of the human family tree. For decades, there were two coexisting theories. The "out of Africa hypothesis" stressed descent of modern humans from a single common ancestor with a growing support for an African origin. The other so-called multiregional theory argued for a multi-linear theory of descent postulating regional origins of modern humans from different ancestral species. With the tides turning in favor of the "out of Africa hypothesis" in the 1980s, the multi-linear model gradually went out of fashion. Following the "fossil explosion," which has seen 11 new species and four new genera named since 1987, understanding of the range of variation in the hominin phenotype was much improved. Two further developments have since revolutionized the empirical base supporting human evolution and emphasized the importance of transdisciplinary enquiry: dating technologies and genetics.

Dating Challenge

There are four primary dating technologies: radiogenic isotopes, paleomagnetism, thermoluminescence, and electron spin resonance. Henry Becquerel, French physicist, discovered the natural radioactive decay of uranium at the turn of the twentieth century. Further work by Ernest
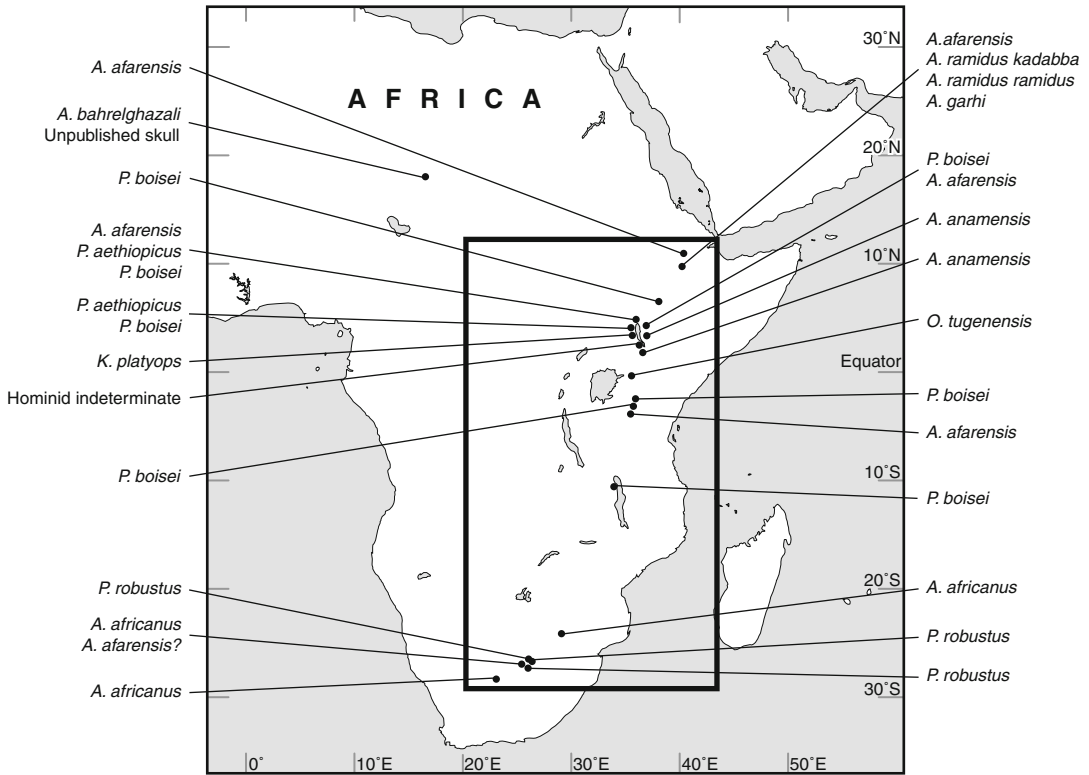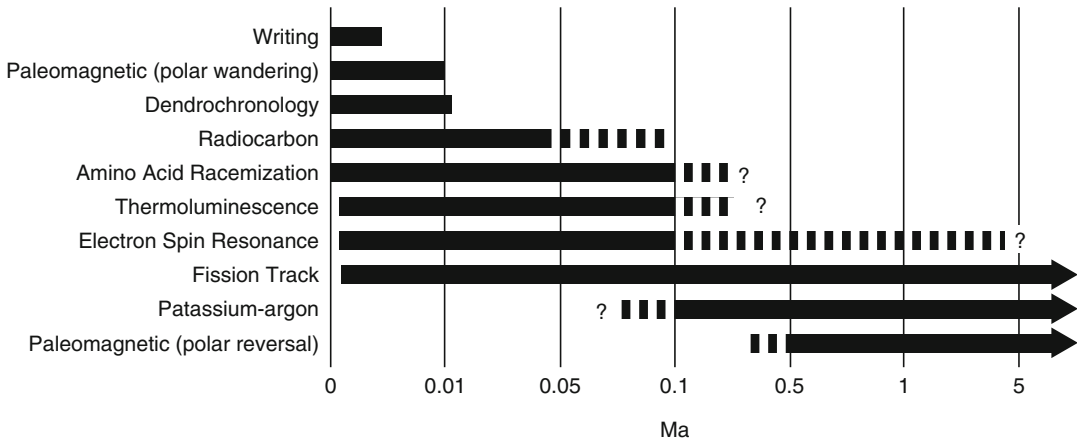
Human Evolution: Theory and Progress, Fig. 1 Map of Africa showing the locations where key hominin species have been found

Rutherford and Bertram Borden Boltwood indicated that the predictable decay of radioactive elements could be used to keep track of time. Not only did it confirm the earth to be billions years old, it provided the earliest empirical time scale for the fossil record. Common chemical elements used in dating include Argon, Carbon-14 (radiocarbon), and Uranium (Fig. 2). Which elements researchers use depends on how quickly they decay. For example, Carbon-14 dating is extensively used to date organic finds 60 Ka and younger as it has a relatively short half-life (the time it takes for one half of the atoms in Carbon-14 to disintegrate) of about 5,730 years. It has allowed us to accurately document the origins of agriculture, around 12 Ka ago, by dating the remains of animals and plants (Zeder 2011). Argon in contrast has a longer half-life and is extremely useful in dating finds older than 10 Ka. Argon-Argon dating has been used to date many of the fossil sites in East Africa and was also used to date hominin remains at Dmanisi in Georgia to 1.8 Myr old (Garcia et al. 2010).

Paleomagnetism uses the direction of magnetic particles in layers of sediment and compares these to the known shifts in the Earth's magnetic field over time. These shifts can be full reversals when the north magnetic pole suddenly becomes the south magnetic pole, or smaller changes in direction due to the magnetic pole wandering and variations in magnetic field strength. Most fossils are found in sedimentary rock which can be difficult to do date using radiogenic isotopes, and this is where paleomagnetism is a powerful alternative. Paleomagnetism was used to date *Sivapithecus*, a genus of extinct primates and probable ancestor to orangutans, to 12.5 Ma (Kappelman 1993). In this case, the

Human Evolution: Theory and Progress, Fig. 2 Effective ranges of major dating methods relevant to human evolution studies

paleomagnetic resolution exceeded the typical 5 % error rate associated with radiocarbon (potassium-argon) dating.

Thermoluminescence and electron spin resonance (ESR) measure the amount of electrons that get trapped inside a rock or fossil over time. First developed in the 1950s, thermoluminescence works on the basis that crystals, such as quartz, trap electrical charges (electrons) at a known rate over time. If this crystal, for example, a flint blade, is heated, these electrons are liberated, emitting a measurable amount of light. This allows researchers to determine when an object was last heated. What is actually determined is the amount of elapsed time since the sample had previously been exposed to high temperatures. It is used to date volcanic materials and meteorite impact craters, but can also directly date past human activity such as when ceramics or flint materials were heated to improve strength and durability (Richter 2007). ESR also measures electrons trapped in the lattice, but unlike thermoluminescence, it does not destroy the sample being tested; this allows samples to be dated multiple times. ESR mostly tests calcium carbonate in limestone, coral, fossil teeth, molluscs, egg shells, quartz, and flint. Both methods are typically used to date samples from the last 300,000 years though theoretically they could be used on much older samples.

Genetic Revolution

Since the 1960s, the field of evolutionary genetics has arguably made the greatest impact upon human evolutionary studies. Advances in technology such as the development of the polymerase chain reaction (PCR) have been instrumental allowing, for example, the analysis of ancient DNA taken from Neanderthal fossils (Green et al. 2010). Allan Wilson, Emile Zuckerkandl, and Linus Pauling pioneered the use of molecular approaches, which examined evolution at the scale of DNA and proteins showing that relationships among living and extinct primates can be inferred from genetics as well as fossils. Genetics too can be used as a "clock," which compares the amount of genetic differences (mutations) between living organisms. Since mutations have predictable rates of change over time, they can be used to estimate how long ago a living species shared a common ancestor. The molecular clock cannot assign concrete dates and must be calibrated against independent evidence, such as the fossil record. Nevertheless, taking together the transdisciplinary evidence, we now have a robust understanding of the relationships between humans and apes. For example, we know that humans and chimpanzees split from their common ancestor approximately 4–8 Ma (Sarich & Wilson 1967; Gagneux & Varki 2001) and that the

genetic difference between humans and chimpanzees is miniscule at about 1.2 %.

Genetics has also confirmed that living humans have a limited genetic diversity indicating a series of population bottlenecks (temporary, drastic reductions in population size and therefore genetic variability, caused by earthquakes or disease, for example) and a limited ancestral gene pool (Foley 1994; Manica et al. 2007). Studies of genetic variation reveal that the greatest diversity can be found in African populations. This combined with evidence from female (mitochondrial DNA) and male (Y chromosome) specific histories confirms an African origin for our species and suggests our ancestors migrated out of Africa about 70–40 ka (Cann et al. 1987).

In addition to helping researchers identify phylogeny, demographic history, and dispersal patterns, we can also identify areas of the human genome influenced by natural selection. Functional genes, such as those involved in infectious disease resistance; life history patterns; diet; skin, hair, and eye coloration; human cognition; and even language, have revealed areas of the genome that have been influenced by natural selection in humans (Enard et al. 2002; Tishkoff & Williams 2002; Lao et al. 2007; Preuss 2012).

Key Issues/Current Debates

The contemporary science of human evolution is an interdisciplinary endeavor encompassing anatomy, anthropology, archaeology, botany, climate sciences, ecology, genetics including ancient DNA studies and geogenomics, geology, history, linguistics, paleoanthropology, paleontology with related subdisciplines, phylogeny, physiology, primatology, and a number of different disciplines specializing in dating. All these disciplines contribute with data and interpretations. They are also, however, contributing to making human evolutionary studies a theoretically heterodox field. One of the main challenges, therefore, is to correlate data and results from different fields, while managing the differences in perspectives and theoretical traditions.

The increasing theoretical and practical complexity and the abundance of new data have overturned a number of simple scenarios of human evolution, leaving a far more multifaceted understanding of the past 6–7 million years of the human story. This aspect has had a great impact on the key questions in human evolution. Traditionally, in classic studies from the late nineteenth and early twentieth centuries, the main events could be summarized to terrestriality, bipedalism, encephalization, and civilization. Opinion was divided as to the order and importance of these key events, but the general consensus was that understanding what really happened in human evolution depended upon solving these four questions.

Following the increased theoretical complexity, the number of key questions has multiplied and now involves a thorough interdisciplinary understanding of the evolution and functions of adaptation, behavior, bipedalism, brain size, chronology, climate, common descent, evolutionary constraints, culture, dispersal and migration, diet, diversity, ecosystems, extinction, genetics, geography, language, lineage, morphology, ontogeny, phylogeny, species concept, technology, and variation. The answer to these questions includes a number of theoretical assumptions about time, selection pressures and mechanisms, inheritance, speciation, convergence, continuity, and discontinuity.

Take, for example, our changing perception of *Homo habilis* (dating between 2.1 and 1.5 Ma). First identified at Olduvai Gorge in Tanzania by Mary and Louis Leakey in the mid-1960s in the same general area as Oldowan stone tools, this was classified as the earliest member of the *Homo* lineage. Specifically, its name means, "man the handyman." In the 1960s, the existing evidence base and predominant view that tool making was unique to the *Homo* genus was a key factor in how these fossils were classified. In addition to tool use, *habilis* had more "modern" (derived) characteristics, including a relatively larger cranial capacity (680 cm^3), weaker brow ridges, smaller teeth, a higher forehead, and postcranial fossils, suggesting beyond doubt that it was fully bipedal. The reduction in so-called ancestral

characteristics tipped the balance and led paleo-anthropologists to classify it as *Homo*.

Since the 1960s however, more fossil and archaeological evidences have raised doubts about handyman's place in the hominin family tree. New evidence shows that *Australopithecus afarensis* was already using stone tools at 3.4 Ma more than a million years before *habilis* existed. It is also clear that tool making is ubiquitous across the primate order and not confined to *Homo* (Bentley-Condit & Smith 2010; McGrew 2010). Taken alone handyman's characteristics such as the larger brain and smaller teeth were deemed to be more derived traits. However, as more australopithecine species (especially *Au. garhi*) were discovered, the overall body size and shape, locomotion, the masticatory system, and dental wear analyses suggested that *habilis* had an adaptive strategy more similar to australopithecines than later *Homo* (Kuykendall 2003). For these reasons, some paleoanthropologists argue that *Homo habilis* should indeed be *Australopithecus habilis*. Whether or not this is valid depends not only on the fossil evidence, but how a genus is defined and whether phylogeny (evolutionary relationships) should be given precedence over adaptive strategies when defining a genus (Wood 2009; Arsuaga 2010).

As the transdisciplinary evidence base expands, it is not uncommon for (phylogenetic) models to change and whether we assign *habilis* to the genus *Homo* or *Australopithecus* has far-reaching effects in our interpretation of the fossil record as a whole. Indeed a similar debate surrounds the classification of chimpanzees, with some primatologists and geneticists arguing that *Pan* and *Homo* should be considered subgenera of *Homo* (e.g., *Homo homo sapiens* and *Homo pan troglodytes*) on the basis of how we interpret the fossil, archaeological, genetic, and behavioral evidence (Goodman et al. 1998; Aiello & Andrews 2000)

The specific nature of data, evidence produced within specific disciplinary frameworks, and the consequences of using different methods and evolutionary models thus shape our interpretation of the evolutionary evidence.

Role of Theory

Theory has played a central role in the development of our understanding of hominin evolution. By creating theories based on the then current evidence, new sources of evidence can be found with which to test the existing theories. Environmental pressures have long been assumed to play a key role in hominin speciation and adaptation (Maslin & Christensen 2007). The *savannah hypothesis* implicates the long-term trend toward increased aridity and the expansion of the savannah as a major driver of hominin evolution. As opposed to long-term directional trends, the *variability selection hypothesis* advocates the role of environmental unpredictability in selecting for behavioral or ecological flexibility (Potts 1998). However, these hypotheses, which emphasize long-term trends toward either a drier or more variable climate, do not explain the pulsed nature of hominin speciation and migration events. Two alternative hypotheses, however, try to account for the discrete and episodic nature of hominin evolutionary events. The *turnover pulse hypothesis*, developed to explain discrete patterns in ungulate speciation, suggests that acute climate shifts drive adaptation and speciation (Vrba 1988). However, the evidence for this hypothesis is equivocal as the stacked benthic foraminifera $\delta^{18}O$ record, which is thought to represent global climate, does not contain the temporal signatures associated with key events in hominin evolution. A region specific hypothesis, the *pulsed climate variability hypothesis*, highlights the role of extreme wet-dry climate cycles specific to East Africa in driving hominin evolution (Maslin & Trauth 2009).

This last hypothesis is based on the distinct geologic and climate conditions of East Africa. The East African Rift System (EARS), one of the most extensive geological features on the Earth's surface, runs north–south for around 4,500 km from Syria through East Africa to Mozambique. The formation of the EARS had a profound effect on the long-term climate of East Africa. Evidence from carbon isotope records from both soil carbonates (Fig. 3) and biomarkers (*n*-alkanes) extracted from deep-sea sediments provide clear evidence of a progressive vegetation shift from C3 (∼trees and shrubs) to C4 (∼tropical grasses)
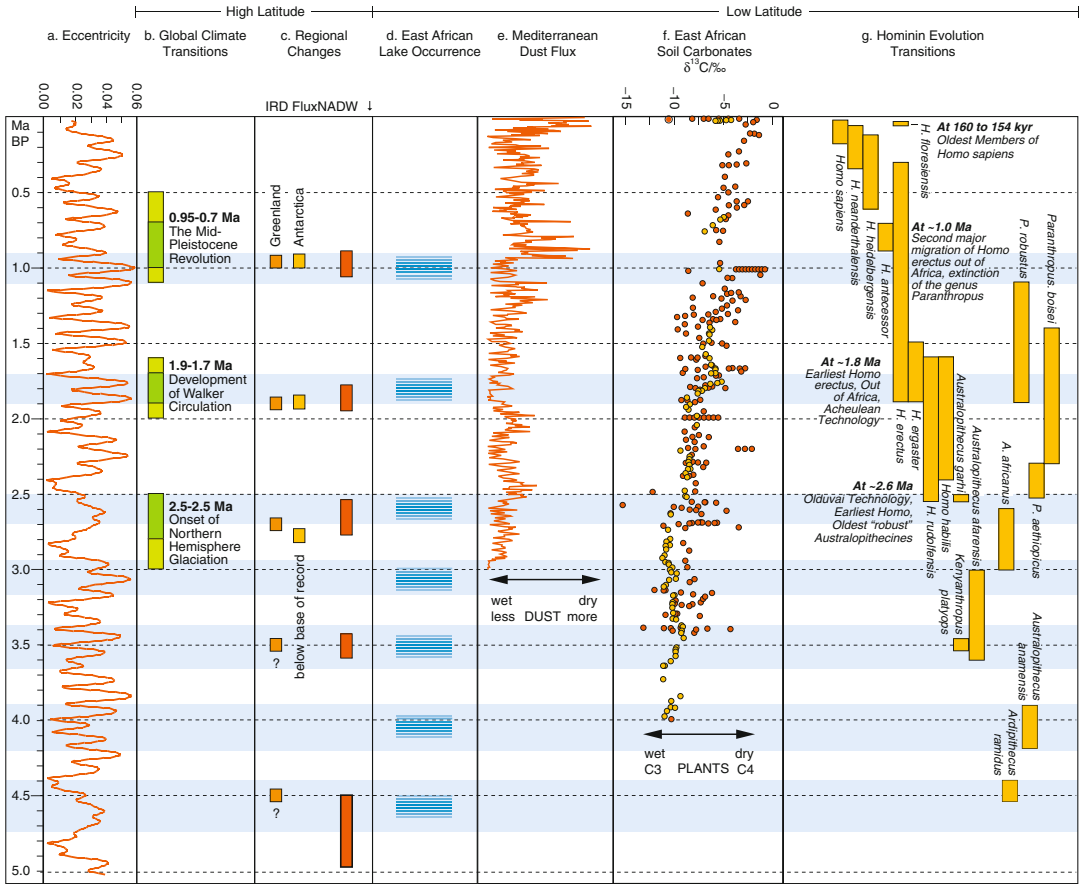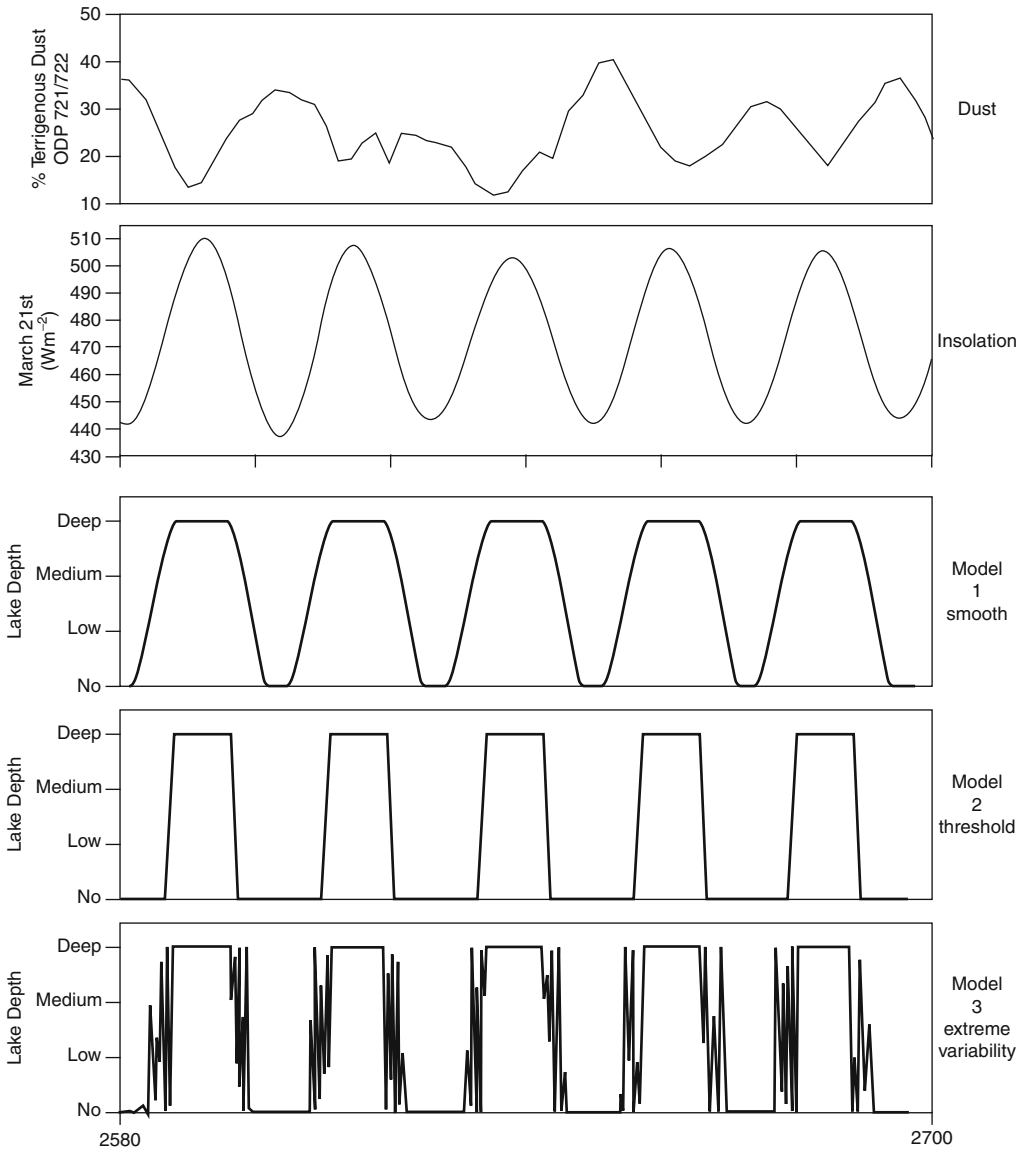
Human Evolution: Theory and Progress, Fig. 3 Environmental context of human evolution in Africa. Comparison of eccentricity variations (*a*) with global climate change (*b*), high latitude climate variations (*c*) with East African lake occurrence (*d*), Mediterranean dust flux (*e*), Soil carbonate carbon isotopes (*f*), with Hominin Evolution Transitions (*g*) (Adapted from Trauth et al. (2007))

plants during the Plio-Pleistocene. This shift has been ascribed to increased aridity due to the orographic barrier produced by the progressive rifting of East Africa during this period and supports the savannah hypothesis, which attempts to explain the appearance of bipedalism.

The progressive formation of the EARS also led to the production of isolated basins within which lakes could form (Fig. 3). Southward propagation of rifting and magmatic activity resulted in the formation of lake basins first in the northern parts of the EARS. For example, fluviolacustrine history of the Afar, Omo-Turkana, and Baringo-Bogoria Basins in the north began in the Middle and Late Miocene, whereas the oldest lacustrine sequences in the central and southern segments of

the rift in Kenya and Tanzania are found in the Early Pliocene. Despite the southward progression of tectonic processes in East Africa, ephemeral deep-water lakes seem to occur in separate basins at approximately the same time, suggesting a climatic control (Maslin & Trauth 2009). There is growing evidence that during each of these major lake phases, the large fresh-water lakes appeared and disappeared on a precessional timescale, and is associated with repeated periods of extremely wet and arid conditions within the EARS (Fig. 4). Up to and including 2.6 Ma, these lakes track 400 ka eccentricity cycles. Subsequently, these lake phases still occur at the peak eccentricity forcing but only at 1.8 Ma and 1.0 Ma, with the most

Human Evolution: Theory and Progress, Fig. 4 Three theoretical models of possible lake changes in East Africa during the Plio-Pleistocene and their implications for the causes of human evolution. 4e Model 1 suggests that there is a relatively smooth and gradual transition between periods with deep lakes and periods without lakes. If this "smooth" model is correct, there may have been prolonged periods of wet or arid conditions, which may invoke the Red Queen Hypothesis or the Turnover Pulse Hypothesis (*TPH*) as possible causes of evolution. Red Queen Hypothesis suggests that continued adaptation is needed in order for a species to maintain its relative fitness among co-evolving systems and that biotic interactions rather than climate are the driving evolutionary forces. While the extreme dry periods would support the TPH which suggests that during arid conditions, selective evolution toward larger, more juvenilized descendants in the bovid lineages and hominins would have occurred. Model 2 envisages a "threshold" scenario whereby ephemeral lakes expand and contract extremely rapidly, producing the very rapid onset of extremely dry conditions required by deMenocal's (1995) "aridity hypothesis." Model 3 is an elaboration of the threshold model in which there is "extreme climate variability" during the rapid transition between deep-lake and no-lake states. Such a model would invoke extreme short-term variability that could drive speciation and extinction events, especially if this climate change occurred over a large geographic region. This would produce the widespread environmental variability as required by the "Variability Selection Hypothesis" of human evolution

significant lake phase at 1.9–1.7 Ma, corresponding with the intensification of the Walker circulation (Trauth et al. 2005). At this time, the E-W sea surface temperature gradients in both the Pacific and Indian Oceans increased intensifying the E-W moisture transport in the tropics, which greatly increased rainfall variability both on a precession and an ENSO (El Niño Southern Oscillation) timescale. The best example of the *pulsed climate variability hypothesis* is the most profound period of hominin evolution at about 1.9 Ma; when there is the highest recorded diversity of hominin species, *Homo (sensu stricto)* appears with brain expansion of up to 80 % and migration out of East Africa into Eurasia occurs for the first time. During this key period, ephemeral deep-fresh-water lakes appeared along the whole length of the EARS, fundamentally changing the local environment. However, it must be stressed that this theory is just one of many in a long history and the more paleoclimate and paleoanthropological data is collected, the theories will continue to evolve.

Environmental theories however can only go so far to explaining why some species thrived and managed to migrate across the globe. The application of environmental determinism should be done with great care especially with hominins for whom at some stage 'social' attributes and behaviours may have influenced morphological evolution. Insights into hominin behavior, mate choice, parental investment, foraging behaviors, and social cooperations which come from the behavioral sciences are thus essential to understand the full range of human evolution. Anthropology, behavioral ecology, economics, primatology, and neuroscience tell us that human life history has evolved gradually, humans are highly cooperative, and reproduction is communal (Tooby & DeVore 1987; Boyd & Richerson 2005).

International Perspectives

Evidence for human evolution is scattered far and wide. The record is certainly not complete overall, but nor is it completely poor. In locations such as the Turkana Basin in east Africa (*Australopithecus, Paranthropus, Homo*), Atapuerca in Spain (*H. antecessor*), and the recent finds on the Indonesian island of Flores (*H. floresiensis*), researchers have collected abundant amounts of fossils and constructed a very in-depth local record. To see human evolution across deep timescales of millions of years however, it is essential to combine multi- and transdisciplinary evidence from all over the world. An excellent example of evidence coming together from all parts of the world is illustrated by evidence for an adaptive shift with *Homo* at around 2 Ma.

This major adaptive shift coincides with *Homo erectus* (1.8 Ma–300 Ka) and we now know that in addition to significant increases in brain size, changes in body shape (relatively elongated legs and shorter arms) which indicated a loss of tree climbing adaptations, innovations in tool technology (earliest handaxes), an ability to walk and possibly run long distances, *H. erectus* had a growth rate similar to that of a great ape with delayed juvenile development, indicating extended periods of learning as well as evidence for care of elderly and weak. They were also the first globetrotters, dispersing beyond Africa, across the Middle East and into Asia (Fig. 5).

However, when *H. erectus* was first unearthed in the form of a skull cap by Eugene Dubois in 1891 in Indonesia, it was the most primitive and smallest brained of all known early human species. This long skull, with a flat forehead, distinct browridges, and saggital keel, was initially placed in a separate genus. Not until the 1950s, by which time many more fossils were uncovered, was it placed into the *Homo* genus. Further discoveries of similar skull caps were made in Zhoukoudian in China and they were initially clearly confined to Asia. It explains the importance of taking the historical context of fossil finds into consideration. At the time, these early fossils were the most primitive known with only Neanderthal specimens in Europe for comparison until the 1920s and 1930s when *H. heidelbergensis*, *Australopithecus africanus*, and *Paranthropus* discoveries started to hint that the human family tree was more complex.
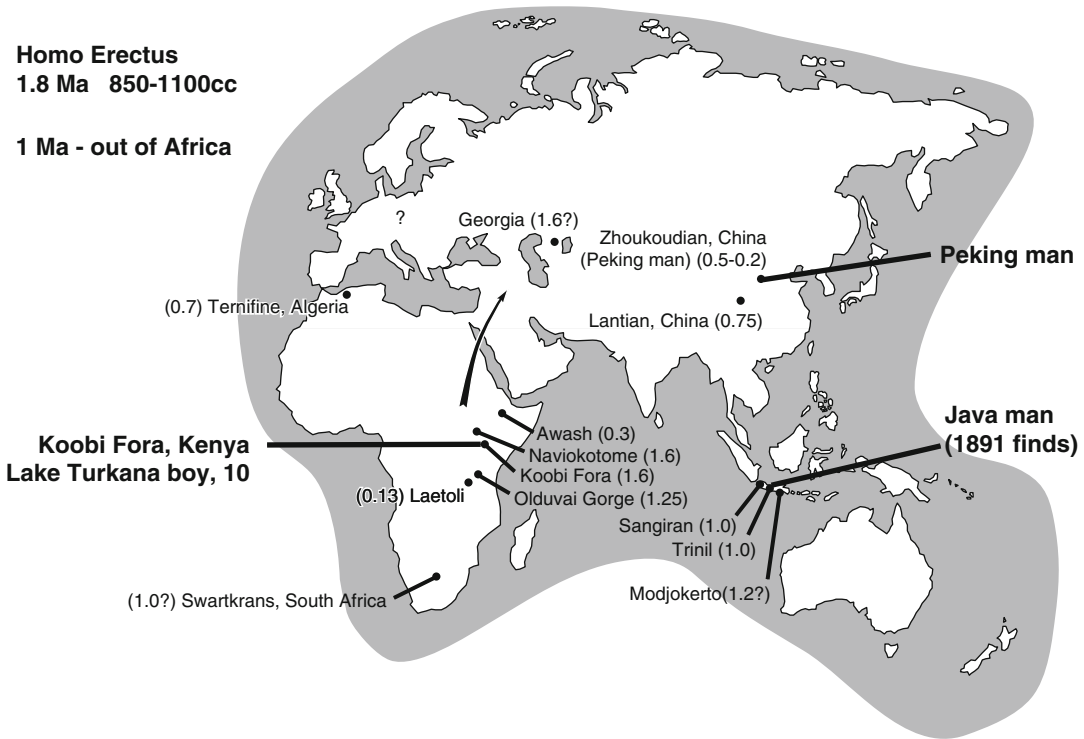
Human Evolution: Theory and Progress, Fig. 5 Dates and location of early *Homo erectus* finds

The fact that we now associate *erectus* with a major shift in the adaptive complex from earlier Australopithecines shown in cranial and dental morphology, behavior, and technology would perhaps startle earlier paleontologists (Wood & Collard 1999; Foley 2002). It demonstrates that human evolution is neither the result of a single revolutionary event nor a smooth accumulation of increasingly modern human features. Instead it is a cumulative process, with novel adaptations arising and disappearing in response to environmental pressures.

A lot more information about erectus body size, shape, and growth patterns came to light in 1984 with the discovery of the Turkana Boy from Kenya. Dated to 1.6 Ma, this near-complete skeleton (sometimes assigned to *Homo ergaster*, it is typically described as the "African erectus") of an 8-year-old male standing relatively tall at 1.60 m suggested that *H. erectus* was not nearly as primitive as previously thought (Fig. 6). A large cranial capacity (880 cm^3 compared to

1,300 cm^3 in modern humans) and tall stature illustrated a dependence on bipedalism, a growing rate (and probable adolescent growth spurt) similar to modern humans. The Turkana Boy made it clear that *H.erectus* originated and persisted in East Africa but left many questions on how, why, and when this species was able to disperse widely not only across Africa, but also in China and Java by 1.8 Ma, though it should be noted that this date is continually revised and it may have occurred slightly later. Evidence is now available from a plethora of fields and provides a solid empirical base to describe and explain the life course of this versatile, global traveler.

H. erectus thrived in a period of major climate change. Combining data from carbon isotope records from soil carbonates and biomarkers extracted from deep-sea sediments, paleo-geologists, -chemists, and physicists have put together a paleo-environmental model which illustrates a progressive vegetation shift form C3 (trees and shrubs) to C4 (tropical grasses) plants during

Human Evolution: Theory and Progress, Fig. 6 Comparison of *Homo erectus* skulls of Turkana boy (Kenya) and Peking man (China)
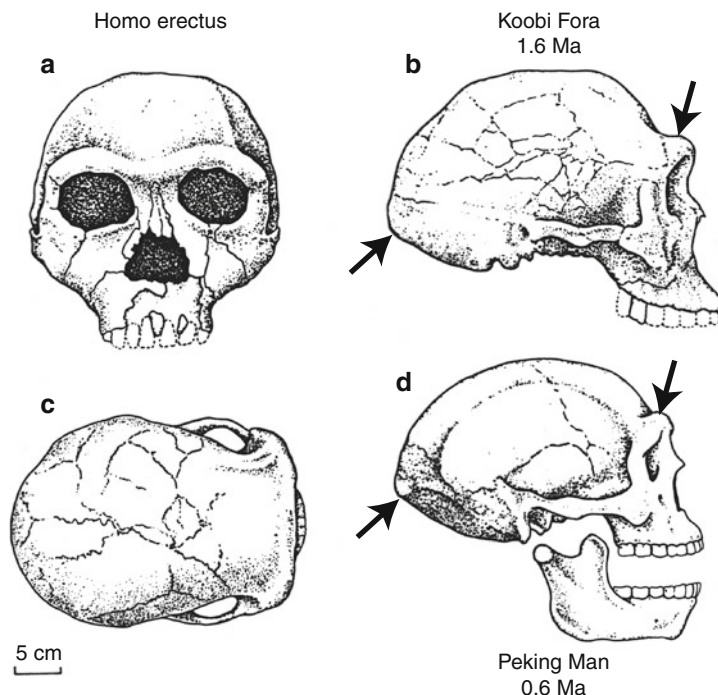
the Plio-Pleistocene. Previously semiarid areas became moister with denser vegetation and more lakes (King & Bailey 2006), making it easier for *H. erectus* to migrate from East Africa into Asia via the "Levant Corridor" through northeast Egypt, Israel, Lebanon, Syria, and Turkey.

In addition to teams from across the world comparing fossil evidence and compiling an environmental narrative in which *H. erectus* evolved, anatomists, primatologists, and ecologists were bringing in their own theoretical paradigms to build up a picture of how *H. erectus* would have survived. Since body size influences a range of physiological traits including energy requirements, choice of food, reproductive strategies, predation risk, range, and locomotor style, paleoanthropologists can learn a lot by comparing *H. erectus* specimens to those of living species. Estimates suggest that *H. erectus* specimens would have been 50 % heavier than australopithecine females. The consequent energetic costs of reproduction, which can be extrapolated based on what we know of human and chimpanzee females, suggest that daily energetic

requirements of gestation and lactation would have been significantly higher for erectus females (Aiello & Key 2012). Human biologists suggest that shortening the inter-birth interval would reduce these costs and increase reproductive output. These changes in life history will have necessitated changes in behavior, for example, increased cooperation and the division of labor. An ability to do so may have been facilitated by language, and evidence from the cervical vertebrae of *H. erectus* fossils from Dmanisi in Georgia shows that they are well within the normal human range, illustrating that erectus was probably able to regulate its breathing and produce complex sounds.

Another way to meet energetic requirements would be to eat energy-dense foods such as meat and technology advances such as the hand ax would have aided *H. erectus* in procuring such foods. The earliest evidence for fire is also associated with erectus fossils, this is significant because cooking food increases the energy availability in foods (Carmody & Wrangham 2009). Alternatively, you could offset the cost of metabolically expensive tissues, such as the brain,

with a reduction in energetic cost somewhere else. The so-called expensive tissue hypothesis is based on comparing gut size across mammals. Anatomists have shown that gut size is highly correlated to diet and shown that the human gut is significantly smaller than expected for an animal of our body size. The expensive tissue hypothesis argues that we have managed to cut energetic costs by reducing gut size because species like *H. erectus* made the move toward hunting or scavenging high-energy and easily digestible meat products (in comparison to plant materials). This allowed an energetic cost saving by reducing the gut size which no longer needed to work so hard. Combining anthropological observations of the Hadza, traditional foragers in Tanzania, with evidence for the erectus' climate-driven adjustments in female foraging and food sharing practices, and longer lifespans, others argue that new social behaviors, such as grandmothers taking care of daughter's offspring, allowed *erectus* to thrive (O'Connell et al. 1999).

Using transdisciplinary evidence from paleoanthropology and primatology to anatomy and biology in combination with the fossil evidence from across the globe, we are now in a position to grasp anatomical, behavioral, and cognitive shifts that accompany the Plio-pleistocene hominins.

Future Directions

There are exciting developments in all fields that are contributing to the understanding of human evolution. We are increasing our understanding of the fossil record and must be prepared for additional surprises such as the discovery of *Homo floresiensis*. In the field of paleoclimate, we understand more and more about the landscape in which our ancestors evolved and how variable it may have been. In the last few years, of all the new fields, genetics has probably had the biggest impact on human evolutionary studies. However, if anything has been learnt from the past, it is that our understanding of human evolution can only occur by combining evidence from multiple fields of study. This way, new theories can be developed and then tested with evidence.

Cross-References

- ▶ Australopithecines
- ▶ Darwin, Charles R.
- ▶ Dating Techniques in Archaeological Science
- ▶ Dubois, Eugène
- ▶ *Homo erectus*
- ▶ *Homo ergaster*
- ▶ *Homo heidelbergensis*
- ▶ Human Evolution: Molecular Timescale
- ▶ Human Evolution: Multiregional Origins
- ▶ Out-of-Africa Origins

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