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Human Origins Studies: A Historical Perspective

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Abstract Research into the deep history of the human species is a relatively young science which can be divided into two broad periods. The first spans the century between the publication of Darwin's Origin and the end of World War II. This period is characterized by the recovery of the first non-modern human fossils and subsequent attempts at reconstructing family trees as visual representations of the transition from ape to human. The second period, from 1945 to the present, is marked by a dramatic upsurge in the quantity of research, with a concomitant increase in specialization. During this time, emphasis shifted from classification of fossil humans to paleoecology in which hominids were seen as parts of complex evolving ecosystems. This shift is in no small part due to the incorporation of neo-Darwinian synthetic theory. Finally, technological innovation and changes in social context are considered as influences on human origins studies.

Keywords Paleoanthropology · History of science · Hominid · Human evolution

Introduction

Considering the grand sweep of history, the realization that human beings gradually evolved from some non-human ancestor represents a very recent insight. Even so, the goal of this one brief essay cannot be to provide an in-depth description and analysis of every significant development

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within the field of paleoanthropology, but rather to identify broad patterns and highlight a collection of "events" that are most germane in shaping current understanding of our evolutionary origin. These events naturally include the accretion of fossil material, the raw data which is the direct, if mute, testimony of the past. These fossil discoveries are situated among technological breakthroughs, theoretical shifts, and changes in the sociocultural context in which human origins studies were conducted. It is only through such a contextualized historical approach that we can truly grasp our current understanding of human origins. Foibles of the past remind us to be critical in assessing newly produced knowledge, yet simultaneously we can genuinely appreciate the enormous strides that have been made.

In addition to selective coverage, a second caveat is that this review will focus on research by scientists writing in English. Non-modern hominids¹ are a cosmopolitan bunch, having been discovered throughout Africa, Asia, and Europe, and there is a significant literature in other languages. In an effort to ameliorate both of these short-comings, numerous secondary references are included in the bibliography, providing more in-depth information on specific topics. For example, some texts approach the history of paleoanthropology by detailing a single time period (Bowler 1986), early human species (Walker and Shipman 1996), or researcher (Morell 1995), and there are

I Hominidae (=hominid) is the biological group (clade) to which humans and their extinct ancestors belong. For many current scholars, this group is distinguished at some lower taxonomic level, usually the tribe Hominini (=hominin). In this study, I maintain the traditional use of Hominidae simply to be consistent with the historical literature. For the same reason, I use the subfamily designation Australopithecinae (=australopithecine) for all of the African "bipedal apes." This group is certainly paraphyletic, to use the modern jargon, and as a result an increasing number of scholars prefer to use the less formal term australopith to lump together the various African species.

quite a few that consider the subject more comprehensively (Leakey and Goodall 1969; Reader 1988; Lewin 1997; Tattersall 2008). In addition, there are a handful of encyclopedia format tomes (Jones et al. 1994; Spencer 1997; Delson et al. 2000), textbooks (Conroy 2005; Cela-Conde and Ayala 2007; Klein 2009), and "coffee table" popular volumes (Stringer and Andrews 2005; Johanson and Edgar 2006) that in part address the history of human origins studies. Moreover, these texts contain abundant references to the primary literature if that level of scrutiny is desired.

In seeking to provide a useful heuristic framework for the purposes of this particular essay, human origins studies can be broken down into two very broad periods. The first is roughly the century between 1850 and 1950 when research, often conducted by individuals with training outside of anthropology, focused on taxonomy and phylogeny. In other words, although scientists were cognizant that climate change (e.g., northern hemisphere glaciations) would have directly impacted the evolution of early humans, they were mainly interested in collecting "missing links," naming them, and creating family trees. The second period, from 1950 to the present, is characterized by the relatively rapid development of paleoanthropology as it is currently practiced. Here the emphasis is only partly on the hominids themselves, with ecological context being of equal importance.

The Emergence of Human Origins Studies

This review begins with two mid-nineteenth century developments which are often conflated, but were initially distinct. The first is the acceptance of a temporal association of human material culture (stone tools), with extinct Ice Age mammals (Van Riper 1993; Sommer 2007). This was significant in that it opened up a considerable prehistory for the human species, well beyond estimates derived from literal scriptural interpretation. However, while acknowledging a lengthy antiquity for the human species, there was, at the time, no reason to suspect that the makers of the stone tools were not fully modern humans in a biological sense. The second major development was the publication of Darwin's On the Origin of Species in 1859 (Darwin 1859). Darwin is rightfully credited with being the most influential, although by no means the first individual to broach the subject of descent with modification, or transmutation theory, as he put it (for an overview of pre-evolutionary ideas related to human origins, see Greene 1959, Bowler 2003). Darwin's central thesis was that all living species shared a common ancestry, with "endless forms most beautiful" having diverged via natural selection, and although he only briefly mentioned his own species the

inference was clear. These two events dovetailed into the now quotidian, but then controversial, notion that humans had evolved over a vast expanse of time (Grayson 1983).

While Darwin was initially reticent to discuss human evolution in any detail, his colleague Thomas H. Huxley harbored no such reluctance when he published Man's Place in Nature: Essays in 1863 (Huxley 1900). Darwin freely admitted that the veracity of his audacious proposal would have to withstand paleontological scrutiny and that his theory would collapse in the absence of transitional fossil forms. Huxley's advantage, beyond his more outspoken personality, was that he actually had a fossil human to describe. The first Neandertal recognized by science was discovered in 1856; however, its description only appeared in English three years later, just as Darwin was going to press (Trinkaus and Shipman 1993). Huxley provided a detailed description of the eponymous cranium coupled with carefully composed line drawings (Huxley 1900). However, while the importance of the Neandertals in providing empirical evidence documenting an ancient and morphologically distinct human form cannot be discounted, these people hardly bridged the gap separating humans and the great apes. Although a few dissenting voices denied the close evolutionary relationship among humans and the "man-like" apes, and consequently an ape phase of human ancestry, most scientists accepted the overwhelming morphological and embryological evidence in support of just such a relationship. This acceptance was in no small part due to Huxley's meticulous comparison of gorilla and human anatomy in which he concluded that the gorilla and its close relation, the chimpanzee, represented the nearest approach to humanity in nature.

If Neandertals were more or less human, then more distant, primitive "missing links" remained to be discovered. Just such fossils were recovered on the island of Java in the 1890s by Dutch physician Eugene Dubois, who had traveled to Indonesia as part of the army but with the express purpose of finding the remains of primitive humans (Shipman 2001). Java Man consisted of a skull cap, a femur, and a few isolated teeth which taken in combination suggested an early human with a much smaller cranial capacity relative to Neandertals or *Homo sapiens* (roughly 1,000 vs. 1,500 cubic centimeters), although the femur appeared modern. Dubois did not receive the universal accolades and acceptance he coveted, but his fossils bolstered the conventional wisdom at the time that humans first evolved somewhere in Asia.

During the early twentieth century, the early hominid fossil record grew significantly, if not exponentially, and evolution was widely accepted in scientific circles even while large segments of the lay public remained skeptical. Certainly, there were disagreements over whether natural selection was a sufficient evolutionary mechanism in itself

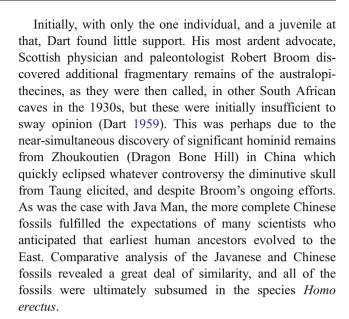


(Bowler 1983), but the basic premise of biological change through time was affirmed. The recovery of additional Neandertal remains in Europe refuted lingering claims of pathology regarding the original Neander Valley specimen and solidified the interpretation that the latter was representative of a population of archaic humans occupying Ice Age Europe. Some Neandertal remains were interpreted as not only indicating intentional internment but also associated funerary ritual. The European fossil record was extended significantly with the recovery of a robust lower jaw from Mauer, Germany discovered in 1907.

In 1912 in England, heretofore devoid of non-modern hominid remains despite the prominence of several British scholars in human origins studies, the announcement of hominid fossils from Piltdown was warmly received locally, if with some incredulity abroad. Piltdown was significant since it reified the "brain first" hypothesis, in which primitive humans evolved a large brain before other key human traits evolved. Although a favorite of intelligent design creationism advocates, Piltdown is actually a beautiful example of the scientific method at work, whereby new evidence eventually calls into question prior interpretation, and in this case recognition of intentional fraud (Spencer 1990). It was, after all, a new relative dating method measuring the fluorine content of fossils that in 1953 exposed the non-contemporaneity of the jaw and skull. In any case, in the first decades of the twentieth century, a fairly simple human family tree was beginning to emerge (see McCown and Kennedy 1972 and especially Delisle 2007 for exceptions). Relatively small-brained Pithecanthropus led to the more capacious Neandertals and Piltdown, who in turn evolved into modern H. sapiens. Yet the truly ape-like human ancestors remained elusive.

Africa as the Cradle of Humanity

In 1921 a skull bearing superficial resemblance to European Neandertals was recovered as part of mining operations at a place called Broken Hill in Northern Rhodesia (now Zambia). Rhodesian Man marks the recovery of the first in a very long line of non-modern hominids from the African continent. A mere four years later, University of Witwatersrand anatomist Raymond Dart, Australian by birth and having been trained in England, published a brief paper describing the fossil skull of a juvenile "ape" discovered in a limestone quarry near Taung, South Africa. Dart identified certain features of the face, the teeth, the cranium, and the brain of Australopithecus africanus that foreshadowed those of H. sapiens and made the startling claim that what was essentially a bipedal ape signaled the beginning of the human lineage separate from the African great apes.



The Neo-Darwinian Synthesis and the New Physical Anthropology

For several disparate reasons, the decades following the end of World War II (WWII) rather quickly led to a science of paleoanthropology that is recognizably modern. One significant factor relevant in the U.S. if not everywhere, was the dramatic upsurge in enrollment at colleges and universities. The G.I. Bill and subsequent effects of Civil Rights legislation that greatly increased access to higher education meant that millions more students went to college and hence the expansion of existing campuses and programs and in some cases the appearance of entirely new colleges and universities². As a result, greater numbers of faculty were required who could teach courses and supervise research in diverse academic programs, which in turn led to an attendant rise in the numbers of graduate students themselves who went on to secure positions at institutions of higher learning. Consequently, many disciplines experienced significant increases in research activity, including physical anthropology, and it is worth noting that this was the first generation of researchers whose formal training was in physical anthropology, not in some allied field such as anatomy or medicine. The dramatic rise in practitioners not only increased the knowledge base in terms of simple quantity, but specialization within the field also began to emerge.



² According to the U.S. Census Bureau, there were about 2.2 million students enrolled in U.S. colleges in 1950. That number doubled by 1963 to just less than 4.4 million and doubled again to over 9 million by 1972.

A second crucial development that transformed human evolutionary studies was theoretical in nature. Changing ideas regarding the process of evolution had been fermenting and roiling in biology circles for several decades before they infiltrated the study of human origins. In essence, a consensus was reached among biologists (sensu lato) that Darwinian natural selection acting on variation arising from random mutation was a sufficient mechanism to explain evolutionary change. For anthropologists, although questions of taxonomy and phylogeny remained important, the intellectual fallout of the so-called neo-Darwinian synthesis led to the "New Physical Anthropology" in which early hominid fossils, rather than representative of some platonic archetype, were interpreted as unique members of variable populations. Focusing on evolution as a process effecting change in populations over time, in contrast to the comparatively myopic sorting of the resulting pattern, arguably represents the most significant theoretical shift in thinking about evolution since Darwin.

Given the comparative de-emphasis on iconic types, the bloated alpha taxonomy of the past was reduced to a mere handful of hominid species displaying previously underappreciated within species variability. This great reduction in hominid names and consequent simplification of hominid family trees has led some modern scholars to lament what they see as a return to the bad old days of teleology and orthogenesis. Yet there can be little doubt that the "splitting" taxonomic philosophy of the past where almost every new specimen received a new species or quite frequently a new genus name was in dire need of revision.

Just as species types came under scrutiny, so did the concept of evolutionary grades which had up to this point made clear distinctions between the categories of ape and human. While this may have provided some welcome taxonomic clarity, it was artificial in that it ignored the evolutionary reality that at some point members of the human lineage *were* very ape-like. This realization, obvious in retrospect, led to the widespread acceptance of the South African australopithecines as human ancestors, and the important corollary that bipedalism preceded other distinctive human attributes (Gundling 2005).

In addition to increased research activity and theoretical shifts, by the early 1960s technological innovations for the first time permitted the creation of a reliable absolute timescale of human evolution. Comparative protein analysis demonstrated that the African apes were most similar genetically to *H. sapiens*, inferring their recent common ancestry to the exclusion of other apes and monkeys. Molecular clocks based upon mutation rates and calibrated by the fossil record suggested that this common ancestor lived as little as a few million years ago, although recent estimates put this ancestor at seven to five million years ago. Consequently, known early and middle Miocene ape

species became suspect as purported human ancestors, since they preceded the split between the hominid and great ape lineages. Most notably this eventually led to the downfall of *Ramapithecus*, a Miocene ape genus once widely hailed as a very ancient and very primitive hominid Lewin (1997).

While molecular studies of living species effectively imposed a theoretical maximum on the age of the hominid lineage, the temporal framework of human origins was further clarified with the introduction of the new potassium argon (K-Ar) method of absolute dating. Louis and Mary Leakey had been scouring the fossil-bearing sediments in and around eastern Africa's Great Rift Valley for decades when Mary discovered the skull of a robust australopithecine at Olduvai Gorge in 1959. Significantly, Zinjanthropus, the genus coined for the new skull, was discovered within sediments near the base of the Pleistocene Epoch. Volcanic minerals from associated strata were dated to approximately 1.75 million years ago using the K-Ar method, nearly double the age estimated from using other more crude means. This greatly expanded time range certainly bolstered claims for the australopithecines as human ancestors rather than extinct collateral cousins to the "true" human lineage, yet to be discovered.

As an aside, Louis Leakey's interest in understanding the human past was not limited to the collection of fossils. Sherwood Washburn, a main architect of the new physical anthropology, along with Irven DeVore, conducted pioneering studies of savanna baboons, large-bodied, terrestrial, and highly social primates that served as living proxies for modeling early hominid behavioral ecology (Washburn and DeVore 1961). Leakey, on the other hand, took a more phylogenetically based approach and hired scholars to conduct research into the behavior of the great apes as a potential new data source informing hypotheses of early hominid behavior. Jane Goodall was the first, studying chimpanzee behavior at Gombe in Tanzania, then came Dianne Fossey who undertook a longitudinal study of mountain gorillas in Rwanda, and finally Birute Galdikas traveled to Indonesia to conduct field studies of the orangutan (see Kinzey 1987 and De Waal 2001 for more recent primate studies that explicitly address questions of human behavioral evolution).

The emergence of paleoanthropology as a truly multidisciplinary endeavor, concerned with a more holistic picture of our evolutionary past, was a logical extension of the post-WWII new physical anthropology which eschewed simple classification and promoted variable populations as the unit of study. Naturally, these hominid populations did not exist in a vacuum but were components of complex, evolving ecosystems. Hence, field work began to emphasize the collection of greater contextual data in an effort to reconstruct biological and physical environments



in which these human ancestors existed and evolved. One of the first field projects to adopt this new approach was an international expedition centered around the Omo River Valley in southern Ethiopia, beginning in 1967. Remarkably, of the 50 papers collected in the resulting volume, only five primarily focus on the hominid remains themselves (Coppens et al. 1976).

Early Human Diet and Subsistence

One major aspect of early hominid ecology that occupied researchers engaged in such multidisciplinary efforts was subsistence, which has understandably been of great interest to paleoanthropologists, particularly after 1950 as scientists endeavored to contextualize the fossil remains of distant ancestors. What early humans ate, how food was acquired and processed, even how it was distributed among members of a social group, became viable questions. Throughout the 1950s and 1960s it was widely assumed that the social, cognitive, and technological skills associated with big-game hunting drove the evolution of the human species; in fact the allure of "Man the Hunter" is longstanding in Western thought (Cartmill 1993). Raymond Dart, as part of his second foray into human origins studies, proposed that Australopithecus had already developed a hunting strategy facilitated by a technology comprised of durable animal parts that he referred to as the osteodontokeratic (bone, tooth, horn) culture. This concept was enthusiastically embraced by writer Robert Ardrey, who published a series of four popular novels documenting the success of these "killer apes" in the context of a changing environment (e.g., Ardrey 1976). Research scientists were only slightly less enthusiastic in championing such ideas (Lee and DeVore 1968) which remain popular, if more nuanced today (Wrangham and Peterson 1996).

Mirroring changes in the broader society, by the early 1970s some anthropologists challenged the "Man the Hunter" hypothesis and developed an alternative that focused on the central role of women in child rearing and gathering of food resources (Dahlberg 1981). These studies used ethnographic data from extant food-foraging societies, the rarity of which injected a sense of urgency on the part of anthropologists. Not long after the "Women the Gatherer" model appeared as a second wave feminist rejoinder to the previously unquestioned authority of "Man the Hunter," another group of researchers also began to question the big-game hunting scenario. Archeologists, geologists, and paleontologists began working on "site formation processes" to get a better understanding of how assemblages of fragmented animal bones and stone tools came to be commingled. Over the next few decades, often with recourse to modern ecosystems as analogs, one of the

main conclusions drawn from the new science called taphonomy (=laws of burial) was the potential importance of scavenging. The association of "bones and stones" was no longer assumed to be the signature of hominid big-game hunting but instead interpreted as meals containing essential fat and protein scavenged by early humans. Perhaps even more disconcerting, some sites were reinterpreted as the remains of carnivore kills occasionally including early humans themselves (Brain 1981; Hart and Sussman 2008).

Here's Lucy

If Mary and Louis Leakey's discoveries at Olduvai put the Great Rift Valley on the map, during the 1970s eastern Africa was validated as the center of early hominid studies. The Leakey's son Richard established himself on the east side of Lake Turkana in northern Kenya, where his expeditions uncovered a prolific cache of early hominid fossils, some of which corroborated the occasionally controversial claims made by his parents a decade earlier. Sediments around the lake yielded hominid fossils of robust australopithecines, early members of genus *Homo*, and an early African variant of Asian *H. erectus*, these days referred to as *Homo ergaster* (Leakey and Lewin 1978). The latter includes a mostly complete skeleton, KNM-WT15000, which has become iconic for the species (Walker and Shipman 1996).

Arguably the most significant fossil discovery of the 1970s was another partial skeleton, AL-288, from Hadar, Ethiopia, better known as Lucy (Johanson and Edey 1981). Here was a single individual represented by numerous skeletal elements, and although her morphology was generally similar to the "gracile" australopithecines of South Africa, she was even more primitive in some respects. Consequently her discoverers coined a new species name, Australopithecus afarensis that included not only the Hadar specimens but fossils collected by Mary Leakey's expedition at Laetoli in Tanzania. The latter is renowned for its famous footprint trail preserved in solidified volcanic ash, imparting convincing evidence for bipedalism at 3.6 million years ago. Hadar is also replete with datable volcanic sediments, and Lucy's status as the most primitive hominid was reinforced by firm radiometric dates which placed the fossils at greater than 3.0 million years ago, at the time astonishingly ancient.

One other significant event from the 1970s bears mentioning. Although the *American Journal of Physical Anthropology* was first published in 1918, it is perhaps surprising that a journal explicitly dedicated to the study of human evolution did not appear in the U.S. until 1972. Since then the *Journal of Human Evolution* has been the premier academic forum for publications related to human



evolution, and in 1992, the Paleoanthropology Society was established, which organizes its own conference and publishes an online journal.

Modern Human Origins

The question of modern human origins has been debated for centuries, long predating paleoanthropology as a scientific discipline. One of the central issues, which became particularly evident as Renaissance and Enlightenment Europeans began to travel the globe on a regular basis, was how to explain the physical diversity of human populations. Two broad perspectives emerged, one which viewed all people as having a single origin and another which believed that supposedly distinct races had separate origins. The pre-Darwinian debates between so-called monogenists and polygenists were recast with the advent of an evolutionary paradigm in the mid-nineteenth century. Within this new theoretical context, monogenists believed that all living humans evolved from a common ancestor that was already H. sapiens, while the polygenists believed that the races had deeper roots and had descended from different non-modern ancestors (e.g., H. erectus or in a few instances different ape species). A major step towards resolving this debate came in 1987 with an analysis of living human mitochondrial DNA diversity which concluded that H. sapiens had a recent African origin. The discovery of essentially modern human fossils at the 160,000-year-old site of Herto, Ehtiopia, provides paleontological support for a recent African origin, and many subsequent genetic studies have supported this basic conclusion. However, the possibility of some gene flow between migrating early modern humans and local archaic populations remains plausible (compare Stringer and McKie 1996 and Wolpoff and Caspari 1998, also see Relethford 2003 for a geneticist's perspective).

Conclusion: Twenty-First Century Paleoanthropology

New fossil discoveries, technological innovations, theoretical advances, and social transformations will continue to inform knowledge of our deep past. Recovery of hominid fossils, some from previously unknown time periods and geographic locations, continues at a brisk rate. Many of the most significant recent discoveries are beginning to fill in the crucial African late Miocene time period during which our lineage ramified from that leading to the chimpanzee (Gibbons 2006). Of particular note, one of these fossils was discovered in Chad, quite a distance from established sites in the Great Rift Valley, challenging the long standing hypothesis that hominids evolved in the savanna grasslands of eastern Africa while the African ape ancestors remained

sequestered in their tropical rainforest refugium. Moreover, botanical, faunal, and geological evidence associated with very early fossil hominids in Ethiopia and Kenya intimate a forested environment, a discovery that clearly constrains hypotheses explaining the success of the bipedal adaptation.

Other significant fossil discoveries from the early Pleistocene site of Dmanisi in the Republic of Georgia have energized discussion of the initial expansion of early humans beyond the tropics of Africa (Wong 2006). Not only are these fossils considerably older than prior known Eurasian specimens, but they are morphologically primitive, especially in terms of stature and cranial capacity, and are associated with very simple ("mode 1") lithic technology. These early migrants hardly manifest the tall striding bipeds equipped with comparatively advanced Acheulian bifacial tools so often depicted in earlier "out of Africa" scenarios³, which are at least in part based on the iconic WT15000 skeleton mentioned earlier.

Perhaps the most surprising discovery of the last decade is the diminutive 18,000-year-old skeleton from the Indonesian island of Flores, which has sparked a spirited, occasionally acrimonious debate between those advocates of a replacement model of modern human origins and those inclined towards regional continuity (Morwood and van Oosterzee 2007). The former, comprised of the team who made the discovery and their allies, interpret the remains as those of a surprisingly primitive hominid akin to early *Homo*, and perhaps the first documented example of the effects of island dwarfing on an early human population. Other scholars believe the remains to be those of a pathological modern human, whose illness resulted in a cascade of skeletal and dental anomalies. Ongoing research on Flores and other nearby locations will undoubtedly resolve this debate.

New discoveries are not limited to the paleontological record but also include behavioral information gleaned from archaeology. Symbolic expression in the form of language, art (including music), and religion is undoubtedly one of the most distinctive human traits. Evidence for such behavior has proved elusive beyond the seeming cultural explosion perceived in the Upper Paleolithic of Europe beginning around 35,000 years before present. However, archeological evidence for at least some of these behaviors has recently been coaxed out of several sites in sub-Saharan Africa. Advanced utilitarian objects such as blades and harpoons have been recovered well back into the Middle Stone Age and use of ochre and shells for body adornment has been found at sites approaching 100 kiloannum (Balter 2009).

³ I usually avoid this term despite its heavy usage within the scientific community. I believe that the "Out of Africa" trope perpetuates an anti-Africa bias which seems to suggest that early humans, on several occasions, left Africa wholesale as if there was something inherently undesirable about the place. I suppose that "hominid extra-tropical range expansion" doesn't have the same ring, but it *is* more accurate.



Recent advances also include a plethora of technological innovations that have allowed anthropologists to hone traditional inquiries in the areas of dating (e.g., single crystal, laser fusion, argon–argon dating), systematic analysis (e.g., geometric morphometrics), and paleoenvironmental reconstruction (e.g., stable isotope analysis). The badly distorted remains of the spectacular 4.4 megaanum skeleton of *Ardipithecus ramidus* from Aramis, Ethiopia was restored in part using digital imaging technology (Gibbons 2009). Additionally, new technology is facilitating, perhaps even driving, novel questions such as those related to the emergence of the unique human life history pattern.

While fossils provide real-time evidence for human evolution, signals from our ancient past are also encoded into our modern DNA. The groundbreaking work of the 1960s effectively demonstrated our close affinity with the African great apes, and today's genomic analyses comparing humans and chimpanzees are beginning to reveal differences in much finer detail than heretofore possible. Already several areas within the human genome have been identified as having undergone intense selection; these regions may be related to the evolution of the especially dexterous human thumb, reduction of muscles of mastication in the wake of the ability to cook food, the greatly enlarged neo-cortex, and our ability for spoken language.

In addition to modern DNA analyses, ancient DNA analysis has informed the "Neandertal problem" providing preliminary evidence in support of the replacement hypothesis, at least in Europe, whereby modern humans arriving there equipped with Upper Paleolithic technology drove the indigenous Neandertals to extinction. Even more recent genomic analyses, however, suggest that a small but detectable degree of interbreeding occurred when expanding modern human populations emerging from the African tropics encountered Neandertal populations in the Middle East around 120,000 years before present (Gibbons 2010).

In conclusion, our understanding of human origins, like all scientific knowledge, is the result of an ongoing, iterative process. Over the last few decades, the accelerating pace of fossil discoveries and the incorporation of innovative technologies have corroborated and enhanced much of what we already suspected to be true, although there have been a few surprises. No doubt this pattern will continue into the foreseeable future as we slowly, yet inexorably, piece together the circumstances by which our lineage became human.

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