# Darwin and the recent African origin of modern humans

**Richard G. Klein**[1]
*Program in Human Biology, Stanford University, Stanford, CA 94305*

On this 200th anniversary of Charles Darwin's birth and the 150th anniversary of the publication of his monumental *The Origin of Species* (1859) (1), it seems fitting to summarize Darwin's views on human evolution and to show how far we have come since. Darwin famously neglected the subject in *The Origin*, except near the end where he noted only that "light would be thrown on the origin of man and his history" by the massive evidence he had compiled for evolution by means of natural selection. In *The Descent of Man* (1871) (2), he said that addressing human evolution in 1859 would "only add to the prejudices against my views." Satisfied now that those prejudices had significantly receded, he deployed an array of comparative anatomical, embryological, and behavioral observations to argue that people had evolved in the same manner as other species. He emphasized the comparative anatomical details in Thomas Huxley's monograph *Evidence as to Man's Place in Nature* (1863) (3) to substantiate the particularly close evolutionary relationship between people and the "anthropomorphous" apes. He also reiterated Huxley's prescient inference, grounded in the distribution of the especially humanlike African apes, that the last shared ancestor of people and apes lived in tropical Africa.

## Development of the Human Fossil Record

The fossil record now confirms that Darwin and Huxley were right to place human origins in Africa, but when they were writing, fossil support for human evolution was almost absent. The most meaningful exception was the Neanderthal skullcap and associated limb bones recovered by quarry workers from a limestone cave near Düsseldorf, Germany in 1856. Unfortunately, the antiquity of the bones was unclear and there seemed to be a reasonable possibility that the skull came from a pathological modern human. Similar skulls and limb bones from other sites, excavated from layers with ancient stone tools and the bones of extinct animals, eventually showed that Neanderthal morphology was not pathological and that the Neanderthals had inhabited Europe before modern humans. However, the additional fossils appeared only after Darwin's death in 1882 and Huxley's retirement in 1885.

When Darwin and Huxley were active, many respected scientists subscribed to the now discredited idea that human races represented variably evolved populations of *Homo sapiens*. The original Neanderthal skull had a conspicuous browridge, and compared with the skulls of modern humans, it was decidedly long and low. At the same time, it had a large braincase, and Huxley regarded it as "the extreme term of a series leading gradually from it to the highest and best developed of [modern] human crania." It was only in 1891 that Eugène Dubois (4) found the first human fossil that could not be similarly characterized. The specimen was a skullcap from Trinil, Java, and it had a significantly smaller braincase and more primitive features than its Neanderthal counterpart. We recognize it today as the first specimen of the archaic human species, *Homo erectus*. Thirty-four years later, in 1925, Raymond Dart (5) described an even more primitive fossil—a child's skull from Taung, South Africa, that was the first known specimen of an australopithecine. Although scientific recognition of the Neanderthal, Trinil, and Taung fossils was not immediate, they illustrated the basic phases in human evolution that we recognize today. Darwin no doubt would be immensely pleased to see how they have now joined thousands of other fossils that unequivocally document the fundamental course of human evolution.

Modern geology was born in Darwin's time, and with it came indications that the earth must be many millions of years old. Darwin paid special attention to this point, because he knew that great antiquity was required to accommodate the evolution of species. However, even after the discovery of *Homo erectus* and the australopithecines, the time span of human evolution remained uncertain, and many specialists assumed that the last shared ancestor of humans and apes existed no more than one million years ago. The application of potassium/argon dating at Olduvai Gorge in 1961 first pushed the date back to at least 1.8 million years ago (6), and potassium/argon and other numeric dating methods applied to new African sites now place it firmly before 4.4 million years ago (7). Sparse fossils imply that it will ultimately fall between 7 and 6 million years ago (8).

## The Course of Human Evolution

In the absence of fossils, Darwin could not have predicted the fundamental pattern of human evolution, but his evolutionary theory readily accommodates the pattern we now recognize. Probably the most fundamental finding is that the australopithecines, who existed from at least 4.5 million to 2 million years ago, were distinguished from apes primarily by anatomical specializations for habitual bipedalism, and it was only after 2 million years ago that people began to acquire the other traits, including our unusually large brains, that readily distinguish us from the living apes.

The greatly expanded fossil record shows that the australopithecines comprised multiple species, and it suggests that our own genus, *Homo*, descended from one of these about 2.5 million years ago. The oldest flaked artifacts date from about the same time, and it seems reasonable to assume that *Homo* and stone tool technology co-evolved. Darwin was no stranger to scientific controversy, and he would surely not be surprised that despite all we have learned, specialists vigorously debate the precise evolutionary relationships among the australopithecines and *Homo*. Fig. 1, however, presents a phylogeny that most authorities would probably accept as a reasonable working hypothesis. It lists the earliest species of *Homo* as *Homo habilis*, and it implies that by 1.7 million years ago, *Homo habilis* had evolved into the more advanced species known variously as *Homo ergaster* or African *Homo erectus*. Sometime between 2 and roughly 1.6 million years ago, *Homo ergaster* became the first human species to expand from Africa to Eurasia.

Following the initial Out-of-Africa event, natural selection and random genetic drift began to drive populations in Africa, Europe, and eastern Asia in different morphological directions. Morphological differentiation was particularly clear by 500,000–400,000 years ago, and from this time onwards, there were at least three evolving human lineages.

Throughout 2009 PNAS will publish several collections of articles examining various aspects of evolution and evolutionary theory. These collections include In Light of Evolution III: Two Centuries of Darwin; Biogeography, Changing Climate, and Niche Evolution; Out of Africa: Modern Human Origins; Plant and Insect Biodiversity; and Evolution in Health and Medicine.

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[1]E-mail: rklein@stanford.edu.

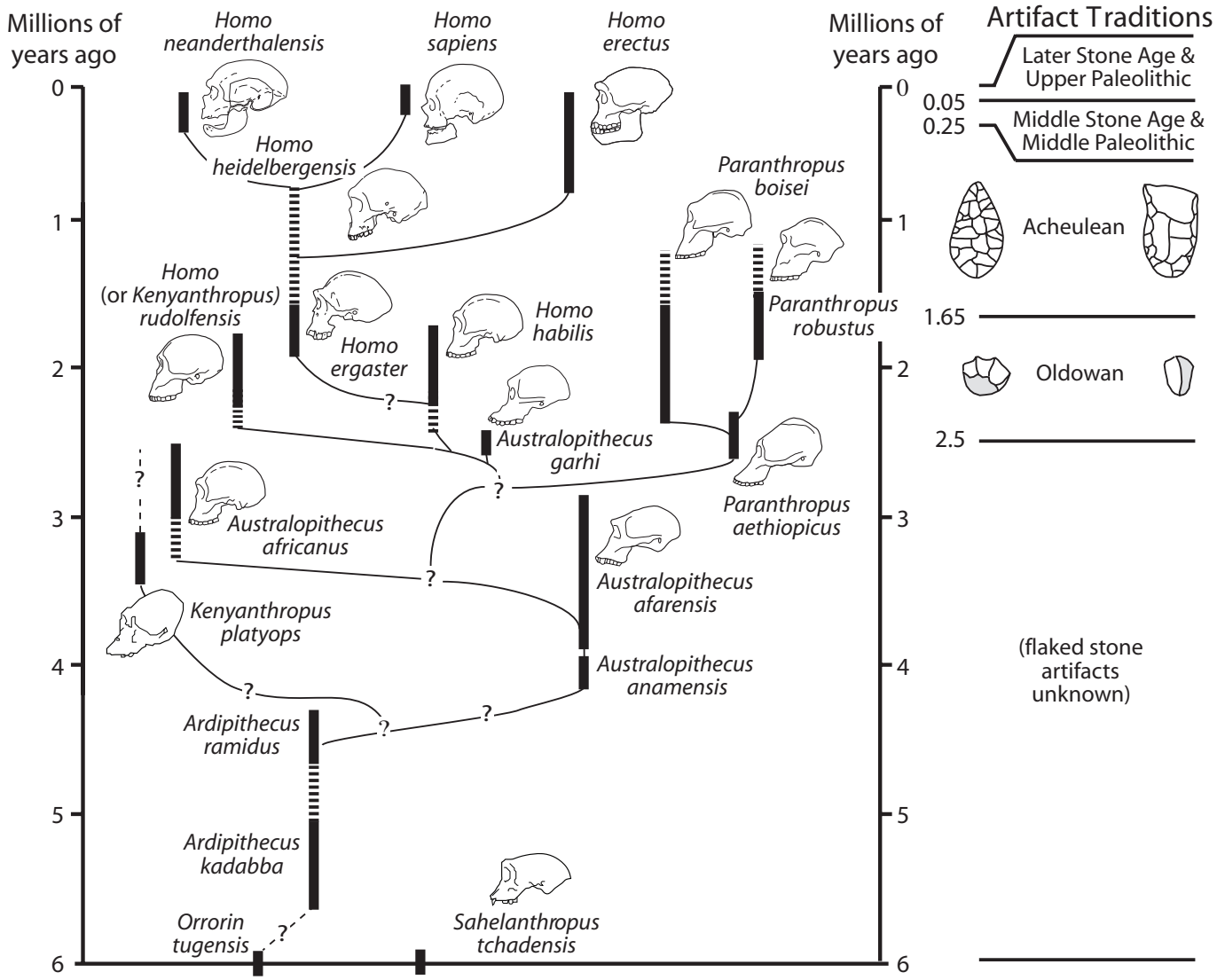


**Fig. 1.** A working phylogeny of the australopithecines and *Homo* (after ref. 19). Flaked stone artifacts appeared at about the same time as the earliest species of *Homo*. The initial expansion of humans from Africa coincided roughly with the shift from the Oldowan to the Acheulean (handaxe) traditions. The subsequent expansion about 50,000 years ago coincided with the shift from the Middle Stone Age/Middle Paleolithic to the Later Stone Age/Upper Paleolithic traditions.

These may always have been able to exchange genes, but distance and small population size probably limited gene flow, and the composite fossil and archeological records indicate that the African lineage spread to replace or swamp the others beginning roughly 50,000 years ago. It is thus reasonable to supply the lineages with biological species labels: *Homo sapiens* in Africa, *Homo neanderthalensis* in Europe, and *Homo erectus* in the eastern Asia. Some specialists would add a fourth lineage for *Homo floresiensis*, a highly distinctive human form that is thought to have existed on the island of Flores, Indonesia, between perhaps 95,000 and 13,000 years ago (9). *Homo floresiensis* is not considered further here, because authorities disagree on whether the principal fossils, a tiny skull and associated partial skeleton, actually represent a distinct species as opposed to a small-bodied modern human afflicted by a growth disorder (10). The issue can probably be resolved only by the recovery of additional fossils and by greater clarity on their temporal and spatial relationship to contemporaneous *Homo sapiens.*

## Out-Of-Africa (Again)

The expansion of *Homo sapiens* from Africa to Eurasia about 50,000 years ago is now known colloquially as Out-of-Africa, although it might better be called Out-of-Africa 2, in recognition of the much earlier human dispersal from Africa shortly after 2 million years ago. The expansion at 50,000 years ago is documented by an extraordinary confluence of fossil and molecular genetic observations, including from DNA ingeniously extracted from Neanderthal bones (11). The genes of living humans imply that the source population for the expansion was probably located in eastern or possibly southern Africa (12), and humans outside of Africa descend from a small number of migrants. This Out-of-Africa founder event was actually just the first in a series of similar events that eventually resulted in the peopling of the world (13, 14). Darwin could never have anticipated the molecular support for Out-of-Africa, but in fact that might be true even if he had died 100 years later, because the seminal molecular study—a kind of tipping point—was published only in 1987 (15). Out-of-Africa is surely one of the great scientific discoveries of the past 25 years, and its acceptance terminated a 100-year debate on the place of the Ne-

anderthals in human evolution. They are now known to have been an extinct side branch of humanity that contributed few if any genes to their modern human successors.

Many details of Out-of-Africa remain to be worked out, and disagreement persists, for example, on the extent to which dispersing modern Africans and archaic Eurasians may have interbred and especially on what promoted the relatively sudden Out-of-Africa expansion. Most authorities attribute the expansion to behavioral changes that conferred a substantial Darwinian fitness advantage, that is, that allowed modern humans of African descent to survive and reproduce at a significantly higher rate than the archaic humans they encountered in Eurasia. However, specialists disagree sharply on how to explain the underlying behavioral shift. Some attribute it to a genetic mutation that promoted the final development of the modern human brain with its seemingly infinite capacity for innovation (16). A larger number ascribe the behavioral change to social, economic, or demographic change, perhaps above all to population growth that increased the frequency and density of transformative interactions among individuals and groups (17).

At the moment, the genetic explanation suffers from the absence of direct evidence for mutational change, although such evidence may emerge when the modern human and Neanderthal genomes can be compared. A draft of the complete Neanderthal genome is expected within months (18). The demographic explanation faces the objection that there is no evidence for population growth in Africa before 50,000 years ago. In fact, human populations became all but archeologically invisible over much of southern and northern Africa in the millennia immediately before 50,000 years ago, probably because of adverse climatic conditions in the middle of the Last Glacial period. To the extent that population growth can be detected in Africa, it came after, not before, Out-of-Africa (16). Continuing archaeological research promises to provide additional crucial demographic details.

The articles assembled for the Special Feature on Out-of-Africa cannot resolve the continuing uncertainties, but they summarize much of the anatomical, archaeological, and genetic evidence that led to its discovery, and they help lay the groundwork for research that should one day explain why it occurred. The answer should intrigue all modern humans, because it will illuminate what it is that makes our species so special.


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