

## Chapter 20 Human Evolution

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### Early Origins

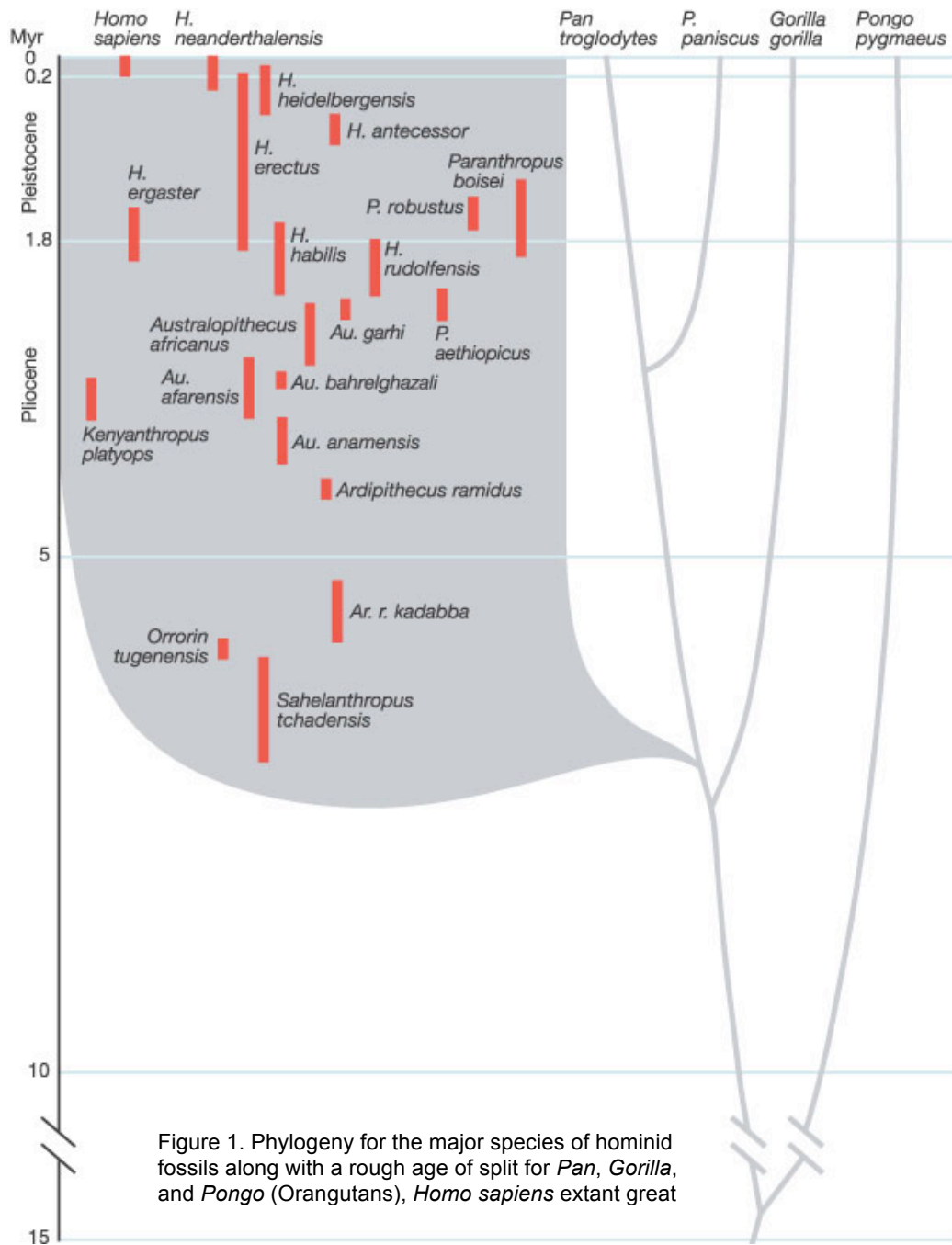
In this chapter, our goal is to gain a sense of time regarding the events leading to the evolution of the complex set of behaviors exhibited by human species. We begin our story in the depths of prehistory when the hominid lineage separated from the other great apes at least 6 million years ago. A remarkably well preserved set of fossils from *Ardipithecus ramidus* including one individual with a nearly complete skeleton were discovered by White et al. (2004, 2008) in Ethiopia. The fossils from the intact skeleton allow us to reconstruct the mode of locomotion and perhaps even the mating system of this ancient hominid.

Approximately 1 my after the Ardi fossils, a new hominid evolved that has been called *Australopithecus afarensis*, which is distinct in possessing a big toe that is no longer opposable but in the modern hominid configuration that is adapted for upright walking. The *Australopithecus afarensis* then gave to two contemporary lineages, the robust and gracile lineages. The robust lineages consisted of two largely herbivorous species (*Paranthropus robustus* and *P. bosei*), whereas the gracile lineages consisted of an omnivorous group of several distinct species such as *A. africanus* and *A. garhi*. The australopithecine lineages date back to 2.6-3.8 million years ago.

A crucial event in the evolution of hominid lineages concerns the origins of bipedalism. We realize of course that all the great apes still use a quadrupedal mode of locomotion. Bipedalism was clearly a set of adaptations involving first the pelvic girdle modifications of *Ardipithecus ramidus* and subsequent evolution of the big toe in its modern orientation in *Australopithecus afarensis*.

### When did bipedalism evolve?

The fossil record speaks loudly on this point. First, functional anatomy of the nearly complete skeleton of Lucy indicates a pelvic architecture that is clearly on the way to bipedalism if not largely



discovery of 3+ million footprints that bellow to an australopithecine. It shows a bipedal set of footprints with a prominent heal mark, large big toe that is in-line with the long axis of the foot (in contrast with ape footprints). Our ancestors clearly evolved bipedalism early. The evolution of bipedalism may have led a morphological constraint to be freed from selection on one use, and allowed this trait to be elaborated for another crucial use. Bipedalism is a **key innovation** in the evolution of subsequent behaviors, and the evolution of brain size. A **key innovation** is a trait that evolves and is crucial for the subsequent diversification and evolution of other traits that form the hallmark of a group.

We can contrast the bipedalism of Lucy and the more ancestral bipedalism of Ardi with an opposable toe, with the nearest extant ancestors, *Pan* and *Gorilla*. *Pan* and *Gorilla* have a quadrupedal locomtion (when they get moving) and it has been assumed for a long time that this was the ancestral condition for extinct homonins. However, recent comparative data for locomotion by Orangutans indicates that arboreal bipelism is likely to ancestral and that the quadrupedal location of *Pan* and *Gorilla* is in fact derived. Given the bipedal reconstruction of *Homo*, *Australopithecus*, *Ardipithecus*, but quadrupedal locomotion of *Pan* and *Gorilla*, and arboreal bipedality of Orangutans as the outgroup (and many other extinct apes), we can parsimoniously assign arboreal bipedality as ancestral. If we include other apes like the monkeys and babbons, it is clear that quadrapelism for *Pan*, *Gorilla* and baboons is derived relative to the ancestral arboreal “assisted” bipedalism (e.g., arm-assisted). Thus, *Pan* and *Gorilla* have a highly derived mode of locomotion, and Ardi would have simply elaborated on the arboreal bipedality in the terrestrial environment (e.g, better balance, no use of arms).

### What is bipedality so important for the human condition of tool using?

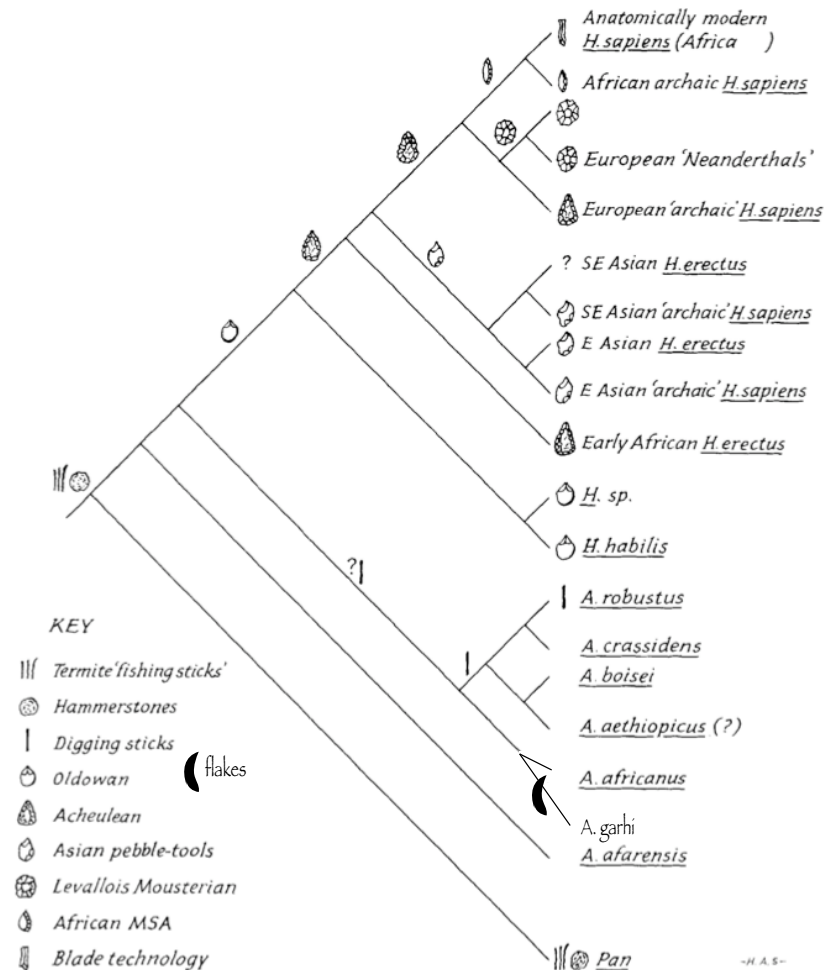
Long hooked fingers were important in locomoting between tree limbs, and a true opposable thumb used for making tools might have required a shift from arboreal to strictly terrestrial modes of

locomotion. In this sense bipedalism is an important requirement for the evolution of opposable thumbs as it releases selection from arboreal functions and allows the development and refinement of the hand for tool use. Our grasping arboreal appendages may have been an exaptation for tool use. An **exaptation** is a trait that evolved for a different purpose than the current adaptive value of the trait. (For example, feathers may have evolved for thermoregulation resulting in an exaptation for flight -- a light insulating structure, which also has aerodynamic properties.) The original use for the hand was in arboreal locomotion, but the function was co-opted for tool use once bipedalism evolved. In this vein, arboreal bipedality is an exaptation for terrestrial bipedality.



Figure 1. A) The locomotion of an Orangutan on flimsy branches is best described as arboreal bipedalism, with an upright posture. B) On stiff branches a quadrupedal mode is used. Even Pan exhibits the upright posture of Orangutans, but only rarely (from Thorpe et al. 2007).

Figure 1. Phylogeny for the evolution of tool use. Notice the flake tools for *Australopithecus garhi*.



### The origin of tool use

As discussed in Chapter 18, tool use is present in *Pan* in the form of termite sticks and large rocks used to open nuts. This behavior is taught matrilineally, from mother to progeny. The tool use seen in

Hominins reflects a great increase in technology, which only occurs through more and more refined intellectual capacity and technological advances that are passed on culturally. Thus genes change and culture advances in lock step. *Paranthropus robustus*, an herbivore, used scapulae from animals to dig up tubers. *Australopithecus garhi* had stone tool flakes associated with their fossil remains. *Homo habilis* develop the first distinctive culture of tools that were clearly fashioned in a stereotypical pattern indicative of cultural inheritance in the fashioning of tools, hence the appellation “handy man”. There is even evidence of between lineage transfer in tool technology, from the *H. sapiens* that were eventually going to displace *H. neanderthalis* in the Dordogne of France (35000 years ago). Eventually, *H. neanderthalis* would be restricted to the Iberian peninsula (30000 ya) and go extinct in Gibraltar (28000 ya).

### When did a large brain evolve?

The fossil record also speaks loudly on this point as we have an excellent series of skulls with which we can compute cranial volumes. However, as there has also been a general increase in body size from the australopithecines (Lucy was sub four feet) to the present, we must correct cranial volume relative to body size. We won't worry about this for the moment as Lucy was just a bit lighter

Table 1 Evolution of brain and body size in hominids

Species	Estimated age <sup>1,3,7,86-88</sup> (Myr ago)	Body size <sup>7</sup> (kg)	Brain size <sup>3,7</sup> (cm <sup>3</sup> )
<i>Homo sapiens</i>	0–0.2	53	1,355
<i>H. neanderthalensis</i>	0.03–0.25	76	1,512
<i>H. heidelbergensis</i>	0.3–1	62	1,198
<i>H. erectus</i>	0.2–1.9	57	1,016
<i>H. ergaster</i>	1.5–1.9	58	854
<i>H. rudolfensis</i>	1.8–2.4	-	752
<i>H. habilis</i>	1.6–2.3	34	552
<i>Paranthropus boisei</i>	1.2–2.2	44	510
<i>Australopithecus africanus</i>	2.6–3	36	457
<i>Au. afarensis</i>	3–3.6	-	-
<i>Au. anamensis</i>	3.5–4.1	-	-
<i>Ardipithecis ramidus kadabba</i>	5.2–5.8	-	-
<i>Sahelanthropus tchadensis</i>	6–7	-	~320–380

This list does not include all recognized species.

(32 kg) than a chimpanzee (45 kg), it's skull was only modestly larger (450 cc) in volume compared to a chimp skull (350 cc), or compared to the cranial volume (500 cc) of the larger bodied gorilla (120 kg). A pygmy chimpanzee has a brain volume of 350 cc and a body mass of 35 kg. This great ape is the closest in body size to *A. afarensis*. This means that australopithecus had a brain roughly  $450/340 = 1.3$  times larger than great apes or 30% larger.

<In lecture, I drew a log-log graph on the board, derived from the facts in the paragraph above and Table 1; see text for slopes >

The proper way to make such comparisons of brain volume relative to body size is to use allometric plots (log-transformed) of brain size relative to body size. If brain volume scales isometrically with body mass, we would expect that these two traits would be proportional to one another. This would imply a slope of one on a log-log plot of brain size relative to body size. If we were to use body height relative to brain volume we would expect these two values to scale with a log-log slope of 3.0 since height is a linear metric, whereas brain volume is cubic linear metric (3rd order measure).

A slope of one gives us a useful "null hypothesis" that we can use for comparing the lineages of great apes, the australopithecines, and the other hominid lineages that arose after the australopithecines -- *Homo*.

The lineages of great apes fall on a line with a slope of 0.34 suggesting that brain size scales with the 1/3 power of body mass.

The lineages of australopithecines fall on a line with a slope of 0.33 which suggests that brain size also scales with the 1/3 power of body mass. Note that the line for australopithecines is higher than the line for the great apes even though both lines have the same slope. This indicates that australopithecines did indeed have larger brains relative to body size compared to the great apes, even though the increase was only 1.3 times larger (see calculations above).

In contrast, the lineages of *Homo* fall on a line with a slope of 1.73. The evolution of brain size in *Homo* lineages greatly exceeded the slope of 1, which would indicate a proportional increase in brain size with body size. Brain size was evolving rapidly from *Homo habilis*, the handy man (2.1 million years ago), to *H. erectus* (~200 kya), to *H. sapiens* in the present.

The relative antiquity of the two hallmarks of the human condition, bipedalism and brain size, do differ somewhat in that bipedalism appears slightly early in the australopithecine lineages relative to the explosion in brain size seen in the lineages of *Homo*. In addition, the origins of expanding cranial capacity are tightly associated with the evolution of tool use in *Homo habilis*. These events can be summarized on a phylogeny in which we plot the various cranial traits and use these traits to reconstruct a phylogeny of the great apes, *Australopithecus*, and *Homo*.

<phylogeny for brain, and bipedal traits plotted in lecture>

<phylogeny for bipedalism reconstructed with the principle of parsimony>

### Neotony and the Evolution of Large Brains

A relatively simple developmental explanation for the evolution of large brains concerns the retention of juvenile characters. Chimp infants have a cranial morphology that is remarkably similar to the modern adult human. Chimps and humans differ in how brains grow after birth. In chimps, the skull (cranial region) does not grow much relative to the face (facial region). In chimps, this results in a greatly elongated facial region, ergo the muzzle of chimps and many apes. In humans, the cranial region continues growing after birth. This growth and proliferation of neural circuits is in a large measure responsible for our greatly enlarged brains. Gould has suggested that we remain "juvenile chimps" well into adulthood, and in so doing we acquire greatly enlarged brains. Many of our learned behaviors are acquired during this greatly prolonged, post-birth, growth of the

brain. The extended parental care found in humans (up to 18 years) is largely unheard of in the animal kingdom. Recall the ideas on [growth and proliferation of neural circuits](#) in vertebrates.

The slope of the **developmental allometry**, or the log-log plot that describes brain development in apes, corresponds quite nicely to the **phylogenetic allometry** that describes brain evolution in humans.

With the sequencing of the human and chimp genome it has been possible to go on powerful fishing expeditions for genes that have been involved in human cortical development. By comparing rates of evolution in all genes in both chimps and humans, any gene with a rate of evolution that is much greater in humans than chimps (relative to background rates in other amniotes) is a candidate for the

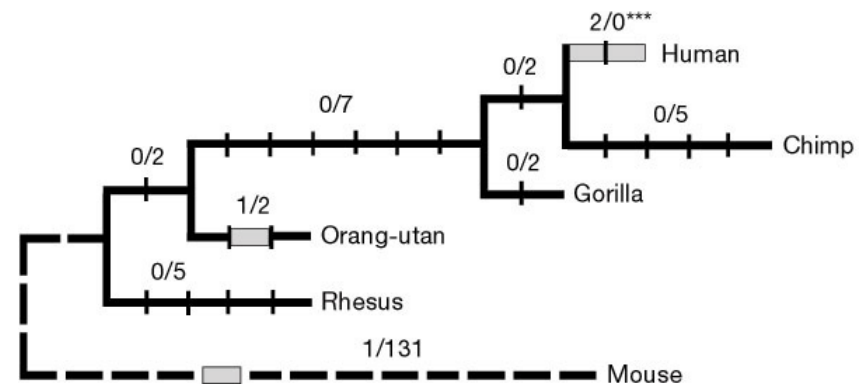


Figure X. Silent and replacement nucleotide substitutions mapped on a phylogeny of primates. Bars represent nucleotide changes. Grey bars indicate amino-acid changes.

changes hominids have undergone since the last common ancestor.

One such gene, FOXP2, has been linked specifically to the development of human language. Mutations that cause a loss of function in FOXP2 disrupt language development. A point mutation

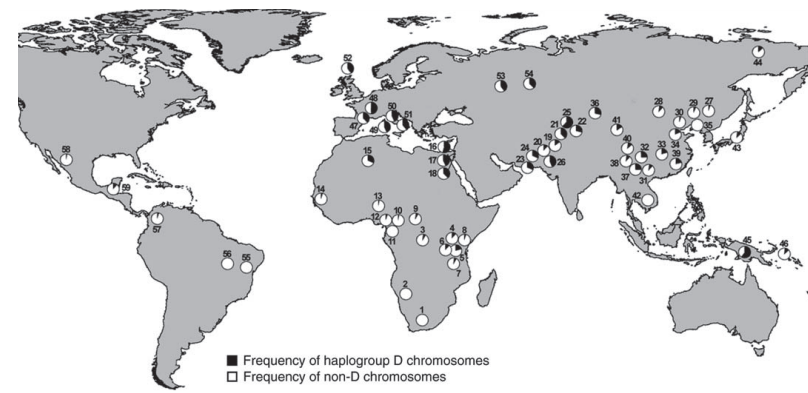


in FOXP2 co-segregates with a disorder in a family in which half of the members have difficulties articulating and impairment in their linguistic and grammatical abilities. Language is a key human trait that is required for the development of human culture. This is a dominant mutation in that two functional copies of FOXP2 are required for acquisition of language. Enard et al. (2002) sequenced the FOXP2 protein in great apes and other mammals, and compared them with the human FOXP2. They show that human FOXP2 contains changes in amino-acids and a pattern of nucleotide polymorphism, which strongly suggest that this gene has been the target of selection during recent human evolution. The number of changes in FOXP2 has accelerated in humans relative to other mammalian lineages.

Pollard et al. (2006) have found another candidate gene, HAR1, which also is localized to the development of the neocortex of humans. The 118-bp HAR1 region a dramatic increase in substitution rate, with an estimated 18 substitutions in the human lineage since the human–chimpanzee ancestor, compared with the expected 0.27 substitutions on the basis of the slow rate of change in this region in other amniotes. The HAR1 gene is specifically expressed in Retzius neurons in the developing human neocortex from 7 to 19 gestational weeks, a crucial period for cortical neuron specification and migration. HAR1F is co-expressed with reelin, a product of Cajal–Retzius neurons that is of fundamental importance in specifying the six-layer structure of the human cortex.

Another approach is to target search for genes that are specifically known to cause developmental abnormalities. For example, microcephaly is a condition in which the neocortex does not develop. Individuals with this specific “**loss of function**” mutation during development do not develop a neocortex. In this case, the lack of function may generate a phenotype that is a putative. While loss of function mutations pinpoint genes that might change, the actual changes in these genes are too large to be useful in understanding evolution of human cortical development. However, a smaller number of mutations over the past few million years or even as short

as tens of thousands of years could accumulate and thereby spread throughout the worldwide population of humans. The gene ASPM (abnormal spindle-like microcephaly associated) is a specific regulator of brain size, and its evolution in the lineage leading to *Homo sapiens* was driven by strong positive selection. Nitzan et al. (2005) screened for small mutations in ASPM that have arisen in the past few thousand years. They surveyed populations across the world for these mutations. They show that one genetic variant of ASPM in humans arose only 5800 years ago and has since swept to high frequency under strong positive selection. These findings, especially the remarkably young age of the positively selected variant, suggest that the human brain is still undergoing rapid adaptive evolution. The origin of this mutation is specifically tied to the same timeframe when humans originated domestication and agriculture and the development of cities and written language.



The search for rapidly evolving gene regions and their subsequent spread illustrates the interplay between interpreting gene evolution in a geographic context. The sampling map for ASPM shows the history of the particular haplotype that spread at an extraordinarily rapid rate (Fig. 20.X). We can actually reconstruct all human origins deeper in time using similar logic.

## Hominid Migration and Diversification

### Mitochondrial Eve Hypothesis and an Out-of-Africa Origin

Our next story begins in prehistoric North Africa. A clan of *Homo erectus* is doing quite well. This clan begins splitting into new groups. We trace the splitting of these clans through timeframes measured in millions of years, and we keep track of one tiny part of the genome. A single female from this clan ultimately gives rise to the rest of the world's Homo, which over the course of the ages are evolving into *H. habilis*, *H. neanderthalis*, and *H. sapiens*.

Let's say we could take a snippet of the mitochondrial genome from all of the females in this clan. The **mitochondrial genome** has a **matrilineal inheritance**, which is to say we all get our mitochondria from our mother (father's do not supply their progeny with mitochondria from the sperm -- it all comes from the mother's egg. One of these *Homo erectus* female's mitochondria would have given rise to all subsequent mitochondria in all other homo lineages. This female would be our **Mitochondrial Eve**. Of course we do not have access to ancient DNA, at least not in these hominid clans.

### How can we reconstruct the hypothetical picture of a single origin for all subsequent homo?

We only have tissue from extant hominids, so we could sample humans from around the globe comparing all the mitochondria in search of a geographic region or race that had mitochondria that was the most ancestral. In this search we are literally trying to find the outcrop mitochondria for homo -- that mitochondria that has the deepest roots in the phylogenetic tree. If we find an area, which possesses such a "root", then all other samples from that area should also root deep into the tree.

This is the logic used by Cahn, Stoneking, and Wilson in a landmark paper on human evolution. They found that a single geographic region possessed such a female -- a region from North Africa.

Moreover, all African samples of mitochondria are rooted very deeply in the clade that was drawn from a sampling of human mitochondria from around the globe.

They found that the roots from the "**most parsimonious tree**" that described the phylogenetic relationship of human mitochondria had deep roots in Africa, the next deepest roots were in Asia, followed by European and New World lineages. The search for a common ancestor for all modern humans had deep roots indeed. From versions of mitochondrial clocks that are termed **coalescence times**, they computed the time at which all these mitochondria coalesced into a common ancestor -- the Mitochondrial Eve. The time was plotted between 180,000-270,000 years ago, which would correspond with a *Homo erectus* representative.

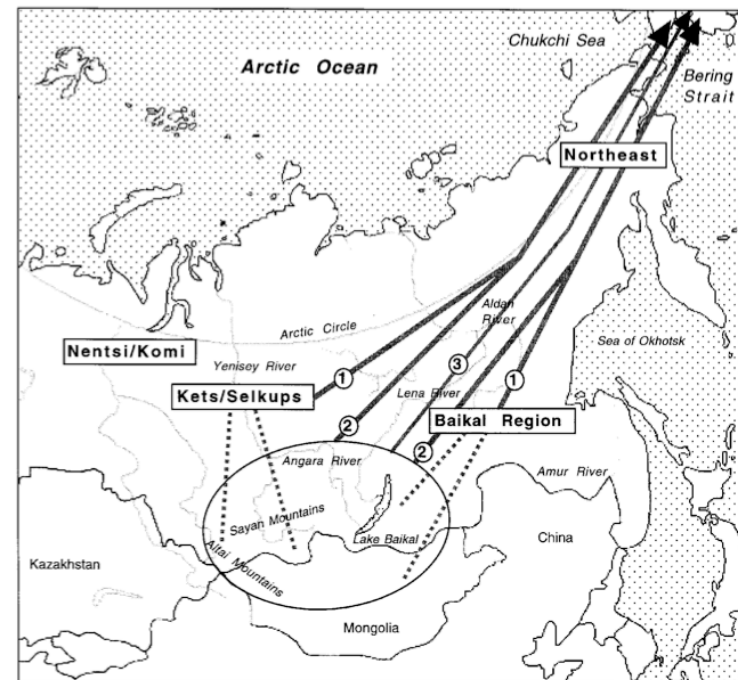


Figure X. Migration from Asia to North America took place at three time points: 10-12K, 6K, and 1.2K years ago as reconstructed with Y-chromosome haplotypes.

The story seemed very nice and it also appeared to unite human ancestry back into the depths of time. This hypothetical clan from North Africa spread from out of Africa to all locations around the globe. Since that time, the lineages could not have experienced much mixing (otherwise we might find lineages of African mitochondrial rooting in Asia, and vice versa. The humans in these regions then evolved in relative autonomy.

More recent recent reconstructions of *Homo sapiens* indicate an expansion about 39000 years ago in a second wave out of Africa. In addition, the use of the Y chromosome Adam has been applied specifically to migration into the new world. Three migrations are recorded: 10-12000 years ago, 6000 years ago and 1200 years ago and these can even be traced to specific populations of origin in Asia (see Figure, previous page)

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### **The Multi-Regional Hypothesis**

Thus, this simple pattern of homo's spread around the globe from an out-of-Africa ancestry was shattered by other reconstructions using Y-chromosome haplotypes (e.g., see Templeton). Templeton specifically used the data from Cahn, Stoneking and Wilson's paper to erect a different hypothesis -- one in which there has been considerable mixing on genes between many different geographic regions. Cahn, Stoneking and Wilson constructed what they believed to be the most parsimonious tree of human ancestry based upon the mitochondrial genome. However, the number of trees that could be constructed from their data set numbers in the billions -- a very big number that would be impossible to search for the single parsimonious tree. There are algorithm's that attempt to find the most parsimonious tree from among the billions. However, these algorithms are fallible. Indeed, Templeton managed to find an even more parsimonious tree that had a strikingly different topology compared to the tree published by Cahn et al.

This tree had Asian lineages rooting very deeply amongst the African lineages, European lineages rooting deeply amongst the Asian lineages. Gone was the nice picture of strictly deep-rooted African lineages. The new picture of hominid evolution was one in which homo might have evolved in either Africa or Asia -- Eve could have come from two places. Moreover, the picture was also messy enough that considerable exchange of genes could have taken place during the subsequent diversification of homo lineages. This led to the construction of the Multi-regional hypothesis for the origins of modern *Homo*. The evolution and diversification of modern homo took place across a large geographic region that encompassed Africa, Asia, and Europe. Exchange of genes through migration took place during the 200,000+ years of modern hominid evolution. There is no exact cradle of origin for the homo lineage -- or so the Multi-regionalists would contend.

The debate rages on as newer and better phylogenies are drawn up that allow for better resolution of the hominid DNA phylogeny. Such information is not restricted to the mitochondrial genome in search of the mitochondrial Eve. The mitochondrial DNA of humans was originally used because researchers needed an area of the human genome that evolved quite rapidly. Because the mitochondrial genome does not have elaborate DNA repair mechanisms like the nuclear genome, rates of mutation in some mitochondrial sequences are an order of magnitude higher than nuclear DNA (an exception to this are the genes that code for the Krebs's cycle which are located on the mitochondria). Researchers have also begun searching for the Y-chromosome Adam. The Y-chromosome has many degenerate regions that evolve quite rapidly. In addition many nuclear DNA regions are being used, foremost among these is the Major histocompatibility loci (MHC). The MHC evolves quite rapidly because these genes are locked in a coevolutionary arms race with all the pathogens that attack humans. Using many genes will allow us to paint a consistent picture of DNA-based phylogenies that should allow us to support or refute the Out-of-Africa or Multi-Regional hypotheses.



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## Cultural Evolution in Humans

The term **cultural transmission** implies a non-genetic mode of inheritance between one generation and the next. This implies that many human behaviors are not necessarily coded for by simple gene, but rather the traits are based on through a form of learning. In the extreme case, we have constructed elaborate libraries in which information is preserved and passed on without direct interactions between the participants of the information transfer.

However, these definitions do not imply that the process of natural selection has not played a role in shaping the evolution of such mechanisms of cultural transmission. Natural selection has played a major role in the mechanisms of cultural transmission:

1. communication,
2. learning,
3. memory,
4. reasoning,
5. technology.

However, because behaviors can be transmitted by genetic and cultural routes our analysis of cause and effect of human behaviors is greatly complicated by this additional possibility. We find ourselves asking questions regarding non-adaptive explanations for modern human behavior because culture can have inertia that transcends genetic changes per se. Many of the modern patterns of human behavior may have purely cultural derivation and such behaviors have no survival or reproductive value. Incest taboos are an example that we might use. Incest taboos do avoid inbreeding, which might be detrimental from the point of view of deleterious mutations.

However, many cultures have moral codes of conduct and incest taboos are built into such morals. Are such morals genetic or are the morals built up by cultural transmission? A society may have devised such laws to keep the culture running smoothly and without conflict. This means that the incest taboos may or may not have a genetic basis. This is a very difficult question to answer. We must think of non-adaptive explanations for behavior in humans (as in bird song!).

A truly adaptive behavior would have the following attributes:

1. variation
2. a genetic basis
3. and demonstrable selection that leads to a change in mean or variance of behavior across generations.
4. finally the trait must have arose as an adaptive solution to a new selective pressure in the environment.

Caution must always be applied to adaptive interpretations of human and animal behavior. We must maintain the same stringent standards in our analysis of human behaviors that we apply to animal behaviors. Little evidence is available on all four points for interpreting human behaviors as adaptive. With this caveat in mind, we begin a class discussion of Adaptive Human Behaviors.

## Study Questions on Human Evolution

1. [Describe the phylogeny for homonins in terms of the origins of bipedalism and brain size. Which came first: bipedalism or brain size increase? Which is the key innovation?](#)
2. Draw a phylogeny for the origin of bipedalism.
3. What is an exaptation? Discuss the evolution of [brain size, bipedalism](#), and [opposable thumbs](#) in terms of exaptations and key innovations? [When did tool use evolve relative to brain size evolution?](#)
4. Draw a phylogeny for the origin of tool use along with specific names of the homonin species and outgroups (and rough time points).
5. Relate the origins of culture in terms of the time points for the switch in purely matrilineal transmission to matrilineal and patrilineal transmission of culture and the switch in mating system. Give both fossil evidence (and time points and species names) and genetic evidence (from mammalian lineages) for mating system evolution in hominids.
6. [Discuss the allometry arguments for the diversification of brain size in lineages of apes, australopithecus, and homo \(supply a graph with correctly labeled axes\). Which lineage has relatively larger brains and why? What is the neotenic theory for the evolution and development of large brains.](#)
7. Discuss the genetic evolution in brain size genes and genes for speech.
8. [Discriminate between Cultural Transmission and Cultural Evolution. Which of these processes is at least in part subject to the laws of natural selection?](#)
9. Discuss the controversy between [nature and nurture](#) of [cultural transmission vs cultural evolution](#). Relate your discussion to the [biological basis of IQ in humans as it relates to the influence of genes and environment](#).