The Homo radiation

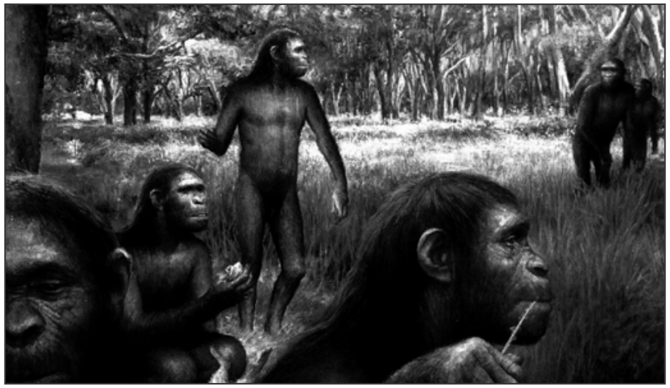
Average 640cm^3 brain compared to 500cm^3 in the Australopithecines

1965-Louis Leakey, Near Olduvai Gorge in Kenya

Homo habilis **– "The Handy Man" – 2.5 Mya? (older than boisei)**
May have had rudimentary language, brain heat exchange

Finds could comprise 2 species (*H. rudolfensis*)

Homo habilis males feeding in East Africa. Two robust australopithecines are approaching. (1.5 - 2.0 Myr ago)



Homo erectus/ergaster

Intermediates between *H. habilis* and *H. sapiens*

Homo ergaster **may have a arisen in Africa 2 Mya and given rise to *H. erectus* (1.8 Mya), maybe outside Africa**

1st *H. erectus* discovered in Java 1891
Pithecanthropus erectus **– "upright ape man" Java man**

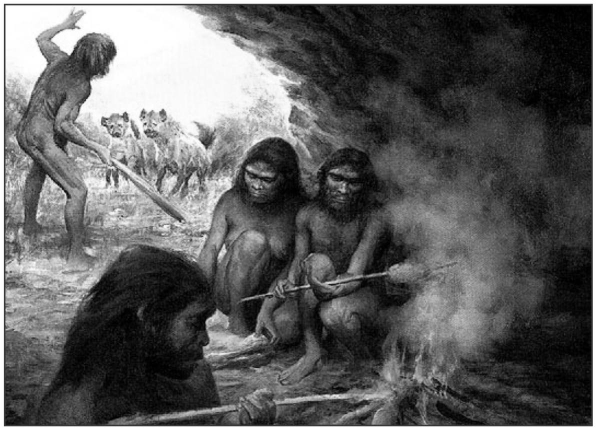
Sinanthropus pekinese **"Chinese man from Peking" Peking man**

Turkana/Nariokotome boy – Kenya – Complete – 6 ft tall (1.6 Mya)

Still have protruding jaw, large molars, excellent biped, sophisticated tools and wide-spread.

Existed until at least 300,000 years ago, maybe more recent

Homo erectus group in Zhoukoudian cave near Beijing in China (250,000 - 500,000 years ago)



Archaic Homo species

<u>*H. heidelbergensis*</u> **(Archaic H. sapiens)**
500,000-100,000 years ago

-intermediate between *H. erectus* and *H. sapiens*, prob. descended from the morphologically very similar Homo erectus.
-the species was tall, 1.8 m (6 ft.) on average, more muscular than modern humans
-larger brain case than *H. erectus* (93%)
-innovated more advanced tools and behaviours

<u>*Homo neanderthalensis*</u>
230,000-30,000 years ago
-larger brain than modern humans
-mid-facial protrusion – cold adapted
-short, solid limbs – very strong
-more advanced tools and weapons than *H. erectus*
-first established burials

A new member of the family

Homo floresiensis
“hobbit”
1m tall
Hunted stegadon

***Nature*, vol 431**


nature

Short for her age

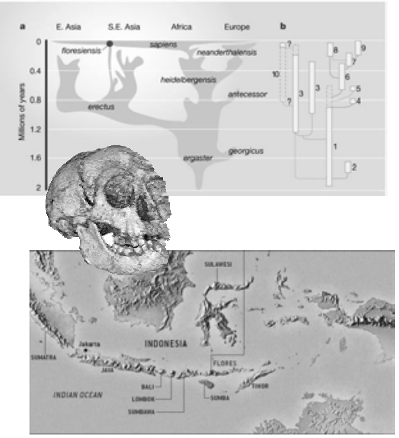
Third Asian *Homo* species reveals diversity of Pleistocene humanity


A species of tiny humans?

This is not a hoax

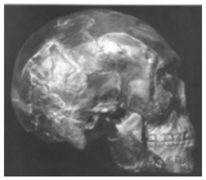
Read the incredible story of Flores Man

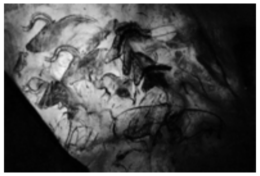
news@nature.com

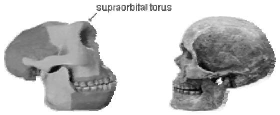


Anatomically modern humans

- **Based on fossil evidence-extent of retraction of face and globular shape of skull**
- **Earliest fully modern human fossils found in Omo-Kibish, Ethiopia and dated 130KYA at oldest.**
- **Despite difficulties in classification and dating, it is clear that AMH appeared first in Africa.**
- **40KYA-Cro Magnon culture**




Chauvet-Pont-d'Arc



The running man?

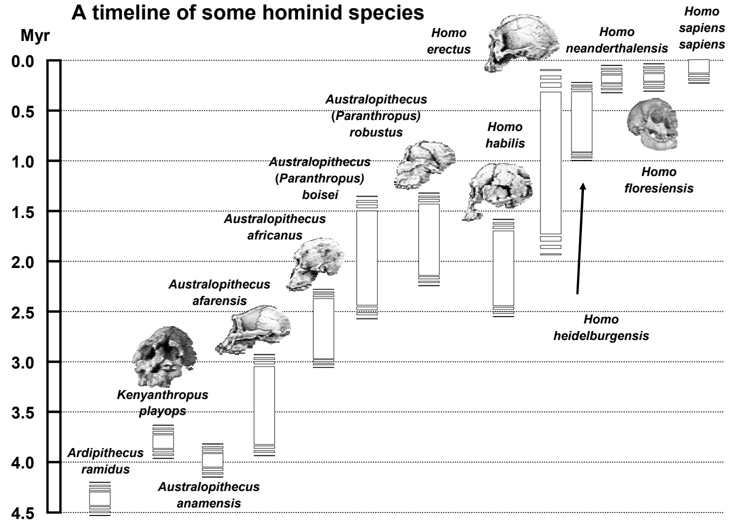

nature

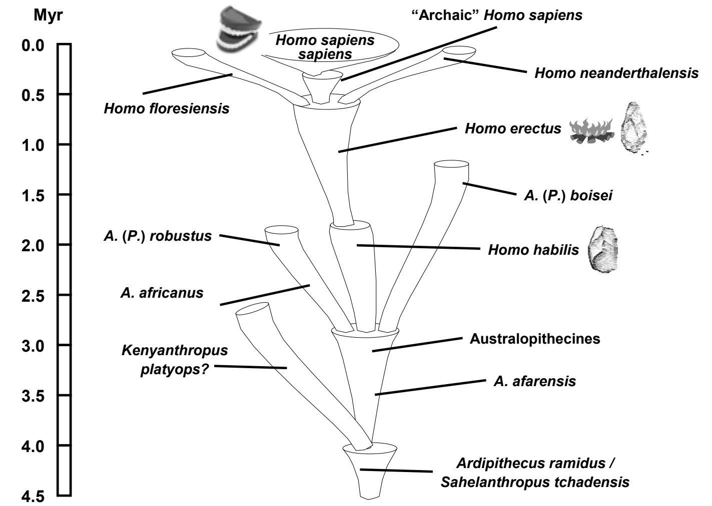
Born to run

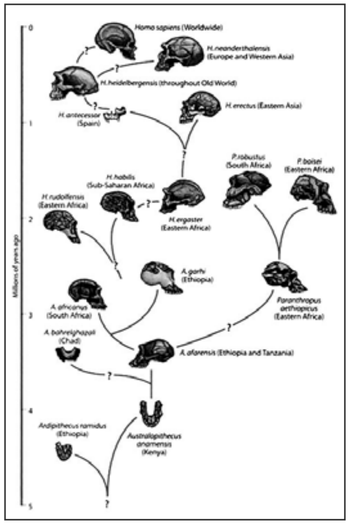
How evolution shaped the modern human

*Bramble and Lieberman, Nature, **432**, 2004.*

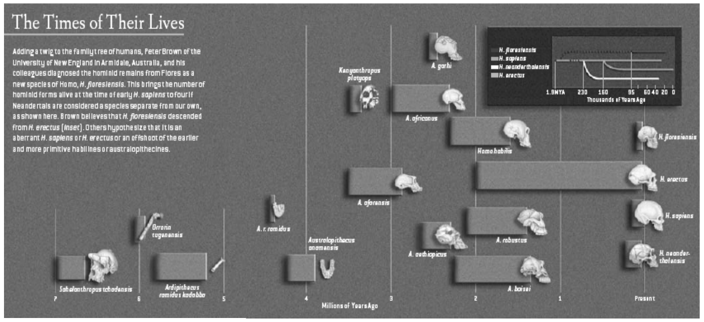
A timeline of some hominid species







Speculative family tree showing the variety of hominid species that have populated the planet. Emergence of *H. sapiens* has not been a single linear transformation from one species into another, but rather a meandering multifaceted evolution.



The Times of Their Lives

Adding a twig to the family tree of humans, Peter Brown of the University of New England in Armidale, Australia, and his colleagues diagnosed the hominid remains from Flores as a new species of Homo, *H. floresiensis*. This brings the number of hominid forms alive at the time of early *H. sapiens* to four if Neandertals are considered a species separate from our own, as shown here. Brown believes that *H. floresiensis* descended from *H. erectus* (*inset*). Others hypothesize that it is an aberrant *H. sapiens* or *H. erectus* or an offshoot of the earlier and more primitive habilines or australopithecines.

Wong, 2005, Scientific American

The origins of *Homo sapiens sapiens*

- Two competing theories to account for the evolution and geographical dispersion of *Homo sapiens sapiens* populations on the globe.

  1) The Multiregional Evolution (MRE) Hypothesis.

  2) Out of Africa Replacement (OAR) Model.

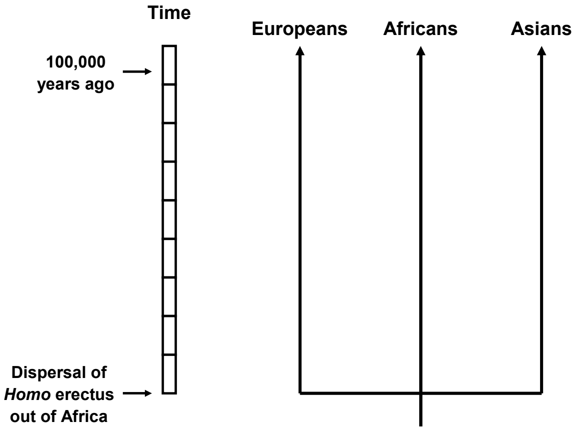
Milford Wolpoff - MRE

Chris Stringer - OAR

The Multiregional Evolution (MRE) Model or Hypothesis

- Modern humans evolved directly from archaic forms such as *Homo erectus* in Asia, *Homo neanderthalensis* in Europe, and *Homo erectus/ergaster* in Africa.
- Gene flow among these populations combined with natural selection for advantageous genes, spread a new modern gene complex globally and maintained genetic homogeneity of the species.
- The MRE model is a more sophisticated version of an older Ancient-Origin Candelabra (AOC) view of human origins. This theory suggested that the divisions among the major Old World geographical groups (Europeans, sub-Saharan Africans and Asians) arose as a result of the spread of *Homo erectus*, followed by the independent evolution of each group into anatomically modern humans (AMHs).
- This extreme AOC version has been thoroughly discredited and has no serious advocates today.

The Ancient-Origin Candelabra Model



Time

Europeans

Africans

Asians

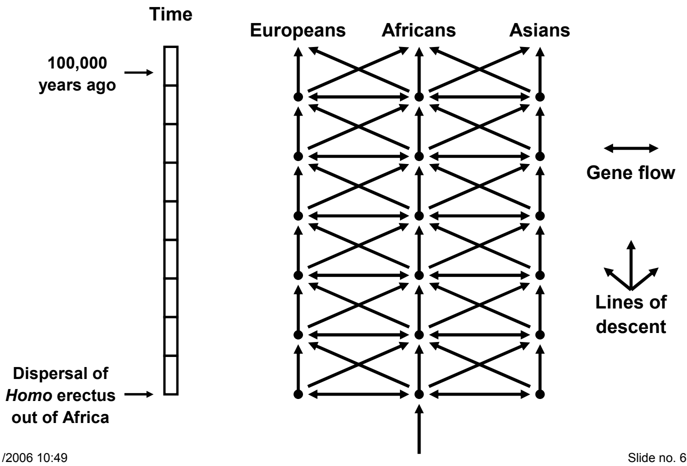
100,000 years ago

Dispersal of *Homo* erectus out of Africa

The Multiregional Evolution (MRE) Model or Hypothesis

- Under the modern MRE hypothesis, our species had hundreds of thousands, perhaps millions, of ancestors for most of the past million years.
- Without a large population, gene flow would have been impossible among populations distributed widely over the temperate and tropical Old World.
- In the MRE model, *Homo erectus* dispersed out of Africa and established populations in Africa and southern Eurasia. These populations were interconnected by gene flow such that there were no evolutionary sublineages of humanity nor independent evolution of the various races.
- The MRE view of human origins is primarily confined to a minority of vocal palaeoanthropologists.

The Multiregional Evolution (Continuity) or Trellis model.


Time

Europeans Africans Asians

100,000 years ago

Dispersal of *Homo* erectus out of Africa

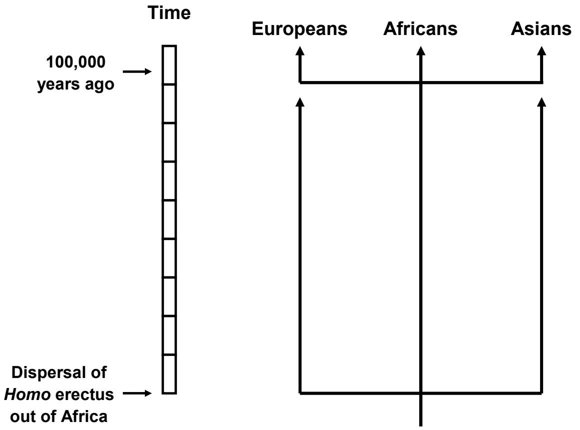
Gene flow

Lines of descent

The Out of Africa Replacement (OAR) Model

- A variant form is proposed where modern humans originated in Africa, but may not have completely replaced archaic forms elsewhere.
- The question of the number of dispersals is also under question. Was there more than one?
- The vast majority of geneticists and most palaeoanthropologists support the OAR in one form or the other.

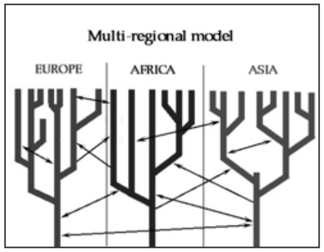
The Out of Africa Candelabra with replacement

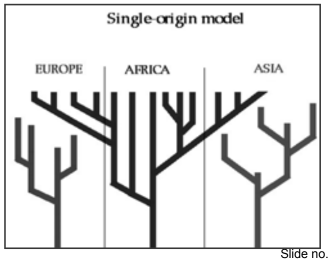

Time

Europeans Africans Asians

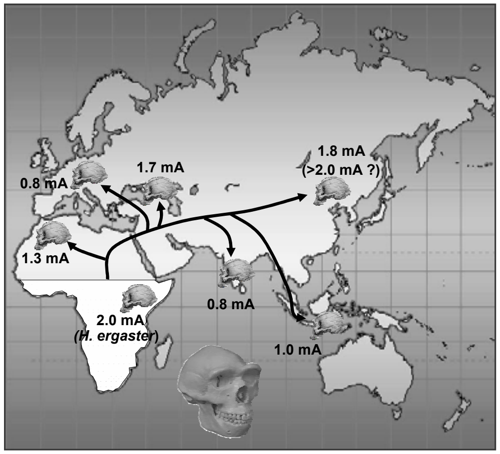
100,000 years ago

Dispersal of *Homo* erectus out of Africa

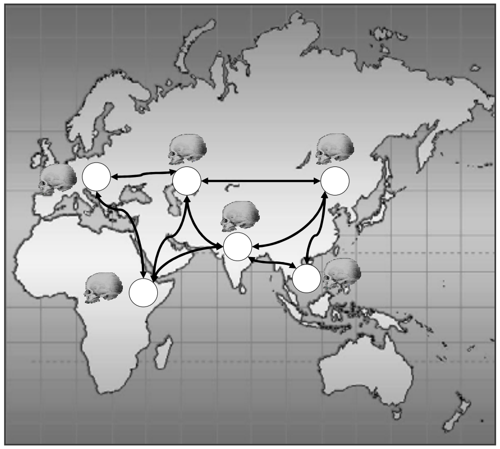




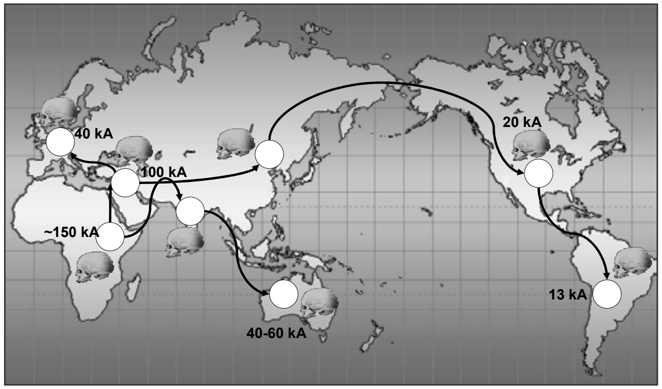
Early-mid Pleistocene migrations of *Homo erectus*



Multiregional evolution (MRE): *Homo sapiens* evolved via networks of gene flow among dispersed *H. erectus* populations during the last one million years.



Out-of Africa Replacement (OAR): *Homo sapiens sapiens* evolved in Africa and migrated across the rest of the globe in one or more waves of dispersal.



Predictions of the MRE model

MRE predictions

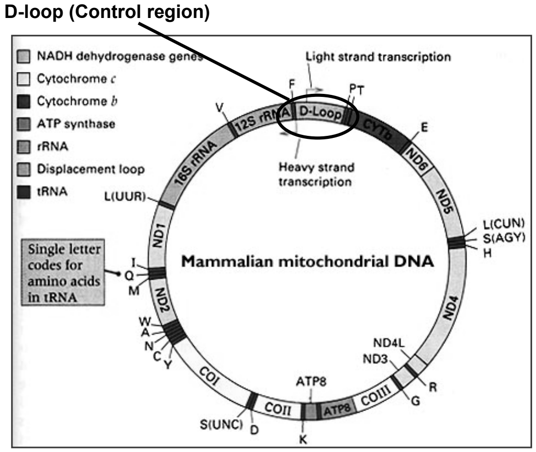
- Our ancestors lived on several continents 1MYA
- Their populations were large enough to facilitate extensive gene flow
- Extensive genetic variation will exist, implying an ancient origin going back at least a million years and possibly two million years.
- No population will show significantly more variation than any other.

Predictions of the OAR model

<u>OAR predictions</u>

- Our ancestors lived only in Africa 1MYA
- Their numbers were restricted
- Only limited variation will exist in modern DNA - implying a recent origin.
- The African population will display the most variation (Asia and Europe are a subset of the variation present in Africa).

Evidence from mitochondrial DNA

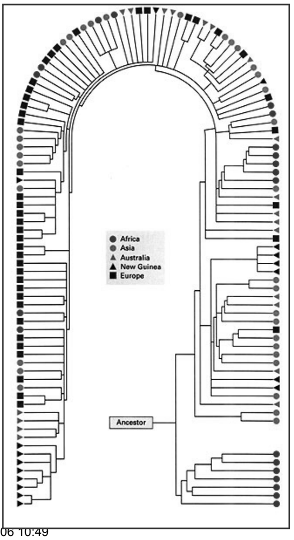


Cann *et al.* (1987) - the first comprehensive mtDNA study

- The first mtDNA study was published in 1987. It gave rise to idea of a Mitochondrial or African Eve. It made the cover of Newsweek in 1988 and that issue was the biggest selling that year.
- The biblical analogy became stretched to the point where it was thought we are all derived from a single woman 150,000 years ago.

Cann *et al.* (1987) - the first comprehensive mtDNA study

- Used 12 restriction enzymes to produce high-resolution maps of the whole mtDNA genome from 147 individuals.
- An average of 370 restriction sites per individual were surveyed, representing about 9% of the 16,569 bp mtDNA genome.
- The 147 mtDNAs mapped were divisible into 133 distinct types (haplotypes).
- They constructed a tree using the 133 haplotypes and the reference sequence.
- Based on known mutation rate (from chimpanzee sequence), they calculated that the common ancestor of all surviving mtDNA types existed in Africa 140,000 to 290,000 years ago (provides support for OAR hypothesis).

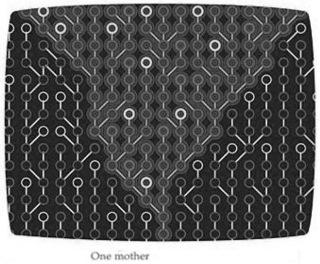


Parsimony tree of 134 human mtDNA haplotypes derived from restriction analysis of whole mtDNA genomes.

Cann *et al.* (1987) - the first comprehensive mtDNA study

- The term Mitochondrial Eve was coined in a newspaper report and quickly became incorporated into the scientific and popular literature.
- This term is misleading. The reason why mtDNA types can be traced back to a single female is not because she was the only woman living then (nor was the population necessarily small), but because the dynamics of loss of mtDNA. All mtDNA types will coalesce back to a single ancestor if you go far enough back in time (lineage loss and extinction).
- Cann *et al*'s conclusion in 1987 merely pinpointed the region of origin of AMH (Africa) and gave an estimate for the time (~200,000 years ago).

Maternal mtDNA lineages in a modern population trace their ancestry back to a single lineage in an ancestral population.



LIFE OF A LUCKY MOTHER: An illustration of the concept that all maternal lineages in a population trace back to a single lineage in an ancestral population. At each generation one-fourth of the mothers will have two male offspring, one-fourth will have two female offspring, and one-half will have one female and one male offspring. The mitochondrial lineages of mothers bearing only male offspring will come to an end, leading eventually to one lineage dominating the entire population. (Courtesy of Allan Wilson.)

Imagine a population of 5000 that remains at constant size.

In the F1 generation:

¼ ♀♀ ½♀♂ ¼♂♂

► ¼ of mothers will leave behind no mtDNA descendents.

10,000 generations to lose all but one.

Important landmarks in the study of human mtDNA variation

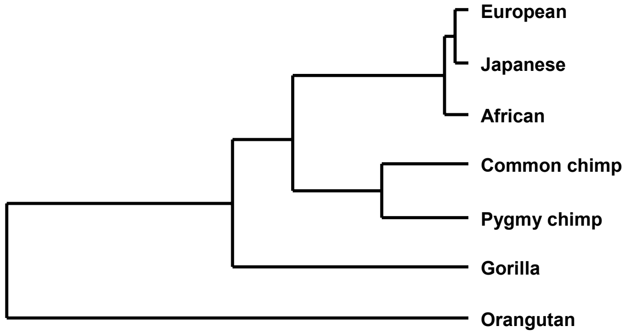
1991	Paper in *Science* from Wilson's lab. It described the sequencing of D-loop sequences from 189 people from major geographical regions of the world (including 121 native Africans). Result - powerful support for OAR. (Vigilant et al., 1991)
1992	Technical comment in *Science* suggested that the statistical and computational methods used by Wilson and colleagues for both the 1987 and 1991 papers were flawed. Only a tiny subset of the possible evolutionary trees from the data had been examined. There are 8 X 10^{264} possible trees that can be derived from the data in the 1991 paper.

Important landmarks in the study of human mtDNA variation

1995 Complete sequencing of the whole 16.5 kb mtDNA molecule from African, European and Asian humans, coupled with sequences from three African apes (chimp, bonobo and gorilla). Strongly supports OAR and gives estimate for the mtDNA ancestor as 143,000±18,000 years ago. (Horai *et al.* 1995).

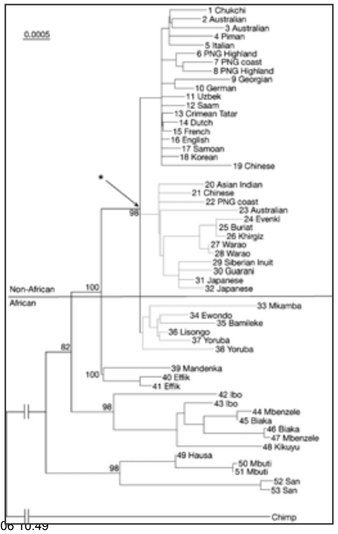
1995 New sophisticated computational methods applied to the original data of Vigilant *et al*. (1991). They were able to home in on the optimal trees (out of 8 X 10^{264} - very powerful computer). They found that the results strongly contradicted the MRE hypothesis and that all the optimal trees had Africans as an outgroup and that the 16 !Kung sequences formed a distinct San grouping (Penny *et al*. 1995).

Phylogenetic tree of whole mtDNA sequences from a range of hominoids



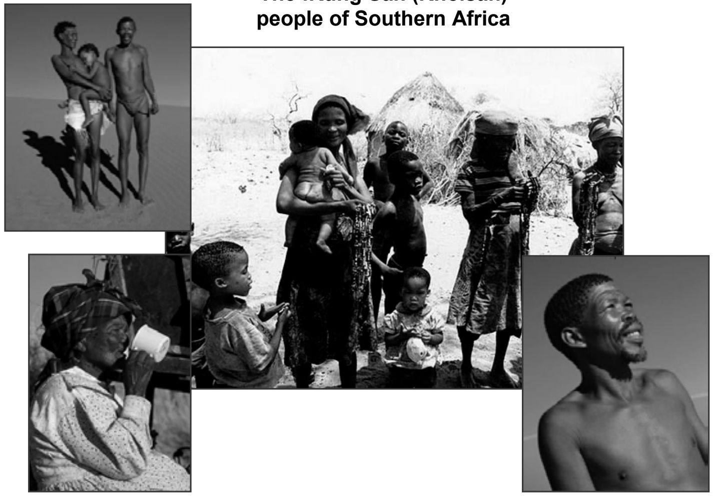
Important landmarks in the study of human mtDNA variation

2000 Survey of whole mtDNA sequence variation from 53 humans of diverse origins. ~172,000±50,000 years for the mtDNA ancestor, 52,000 ±27,500 for an African exodus (Ingman *et al*. 2000). They constructed a neighbour-joining phylogram with several striking features.



- •Complete separation of African and non-African lineages
- •The three earliest branches lead exclusively to Africans.
- •Deep branches within the African phlyogeny, star-like within the non-African lineages.
- •TMRCA for whole phylogeny: 172 +/- 50 KYA
- •TMRCA for branch with Africans and non-Africans: 52 +/- 28 KYA
- •Expansion time for non-African lineages ~38 KYA

The !Kung San (Khoisan) people of Southern Africa



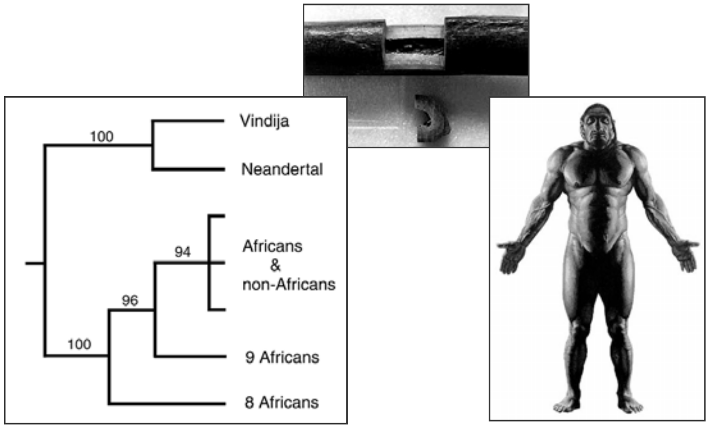
Evidence from Ancient DNA

1997 Krings *et al.* (1997) (Svante Pääbo's laboratory) succeed in extracting DNA from a Neanderthal specimen. Amplified portions of the mtDNA control region (379 bp from D-loop) and compared it to modern human sequences. They compared the sequence to 2051 human and 59 common chimpanzee sequences. There was a substantial difference between the Neanderthal sequence and the panel of modern human sequences.

Modern human sequences differ amongst themselves by an average of 8.0±3.1 mutations. Modern human and the Neanderthal sequences differ by an average of 27.1±2.2 mutations.

Using chimp as an outgroup they were able to estimate the time of divergence between Neanderthal and AMH mtDNA as 550,000 to 690,000. This is approx. four times greater than that of the common ancestor of modern humans.

Schematic phylogenetic tree of two Neanderthal sequences and 663 contemporary humans (Krings *et al.* 1997, 2000).



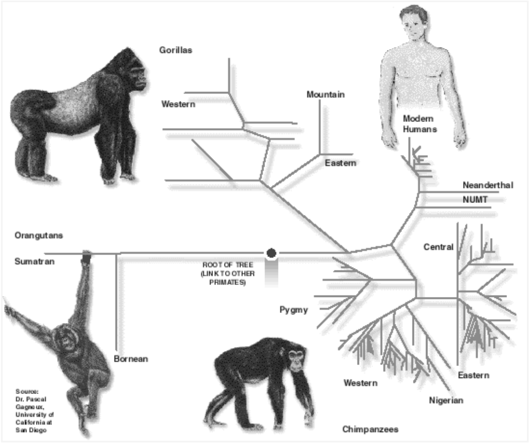
Important landmarks in the study of human mtDNA variation

1999 A large survey of mtDNA variation in humans and African hominoids is published (Gagneux *et al*. 1999). Shows that several chimpanzee and bonobo clades and even single social groups have retained substantially more mtDNA variation than is seen in the entire human species.

2000 Two more Neanderthal sequences from the Caucasus and Croatia are found to be similar to the German Neanderthal sequence. (Ovchinnikov *et al.* 2000; Krings *et al.* 2000).

2004 Currat & Excoffier modelled the likelihood of admixture between AMH and Neanderthals and found that the populations were likely to have been biologically distinct.

Unrooted phylogram of 1,158 control region sequences from African and Asian hominoids (Gagneux *et al.* 1999).



Source: Dr. Pascal Gagneux, University of California at San Diego

---

Implications of mtDNA work for theories of modern human origins

- **The pattern of mtDNA diversity (more diversity in Africa) supports OAR.**
- **The shallowness of mtDNA diversity in contemporary human populations supports the OAR (compared to other hominoids).**
- **The coalescence time to the most recent common ancestor (MRCA) for mtDNA supports OAR (~150,000 years).**
- **The observation that non-African mtDNA diversity is a subset of African diversity supports OAR.**

Implications of mtDNA work for theories of modern human origins

- **The distinctiveness and phylogenetic integrity of the three Neanderthal mtDNA sequences retrieved to-date supports OAR.**
- **The phylogenetically deepest mtDNA branches seem to be within the Southern African San population.**
- **<u>However</u>, mtDNA is only one genetic marker and its unusual mode of inheritance may have masked male-specific gene flow from archaic populations**

RECAP 1

- **Humans are a member of the primate order, and genetic and other molecular studies have shown that they are most closely related to the chimpanzee.**
- **Fossils that date to the approximate time of the human/chimp split (5-7 MYA) have been described but remain to be fully evaluated.**
- **Several hominid were present in Africa from ~4-2 MYA. Most are classified as Australopithecines.**
- ***Homo erectus/ergaster* first appeared in Africa ~2MYA and was the first hominid to migrate out of the continent.**
- **Some later *Homo* species have been described, but their relationships are still debated.**

RECAP 2

- **Anatomically modern humans are first found in Africa about 130KYA, and from 50KYA in other parts of the world.**
- **The Multiregional Theory and the Out-of-Africa theory both sought to explain modern human origins.**
- **Most genetic diversity is found within African populations and most mtDNA phylogenies have an African root, implying an African origin for our ancestors.**
- **mtDNA from *H. neanderthalensis* shows that it is a distinct lineage.**