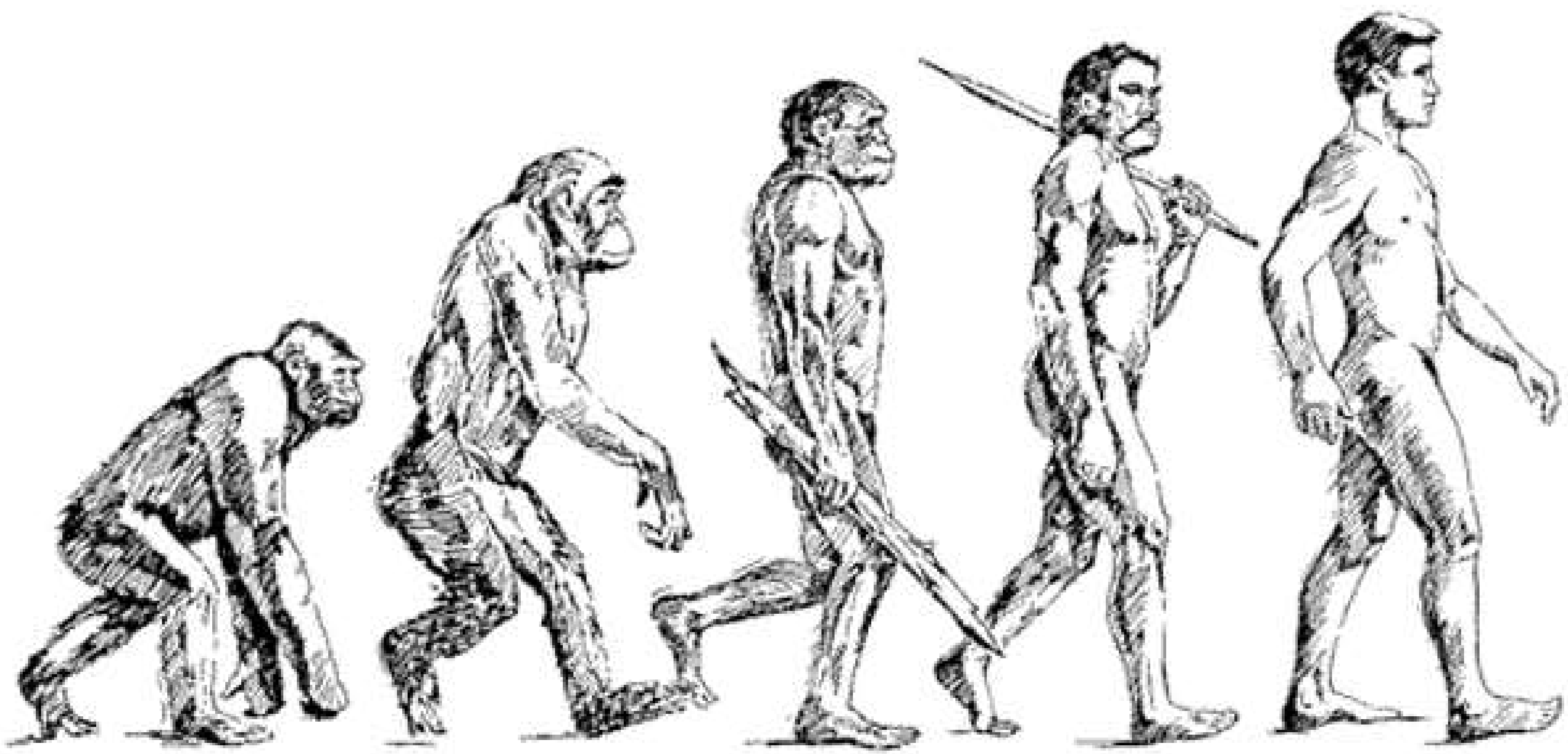
Evolutionary Anthropology & Human Evolution

(Basic Concepts and Applications)



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Human Evolution

Human evolution, or *anthropogeny*, is the origin and evolution of *Homo sapiens* as a distinct species from other hominids, great apes and placental mammals. The study of human evolution uses many scientific disciplines, including physical anthropology, primatology, archaeology, linguistics and genetics.

The term "human" in the context of human evolution refers to the genus *Homo*, but studies of human evolution usually include other hominids, such as the Australopithecines, from which the genus *Homo* had diverged by about 2.3 to 2.4 million years ago in Africa. Scientists have estimated that humans branched off from their common ancestor with chimpanzees about 5–7 million years ago. Several species and subspecies of *Homo* evolved and are now extinct. These include *Homo erectus*, which inhabited Asia and *Homo sapiens neanderthalensis*, which inhabited Europe. Archaic *Homo sapiens* evolved between 400,000 and 250,000 years ago.

The dominant view among scientists concerning the origin of anatomically modern humans is the "Out of Africa" or recent African origin hypothesis, which argues that *Homo sapiens* arose in Africa and migrated out of the continent around 50,000 to 100,000 years ago, replacing populations of *Homo erectus* in Asia and *Homo neanderthalensis* in Europe. Scientists supporting the alternative multiregional hypothesis argue that *Homo sapiens* evolved as geographically separate but interbreeding populations stemming from a worldwide migration of *Homo erectus* out of Africa nearly 2.5 million years ago. This theory has been contradicted by recent evidence, although it has been suggested that non Homo sapiens Neanderthal genomes may have contributed about 4% of non African heredity and the recently discovered Denisova hominin may have contributed 6% of the genome of Melanesians.

History of ideas

The word *homo*, the name of the biological genus to which humans belong, is Latin for "human". It was chosen originally by Carolus Linnaeus in his classification system. The word "human" is from the Latin *humanus*, the adjectival form of *homo*. The Latin "homo" derives from the Indo-European root, *dhghem*, or "earth".

Carolus Linnaeus and other scientists of his time also considered the great apes to be the closest relatives of humans due to morphological and anatomical similarities. The possibility of linking humans with earlier apes by descent only became clear after 1859 with the publication of Charles Darwin's *On the Origin of Species*. This argued for the idea of the evolution of new species from earlier ones. Darwin's book did not address the question of human evolution, saying only that "Light will be thrown on the origin of man and his history".

Fossil Hominid Evolution Display at The Museum of Osteology, Oklahoma City, USA.

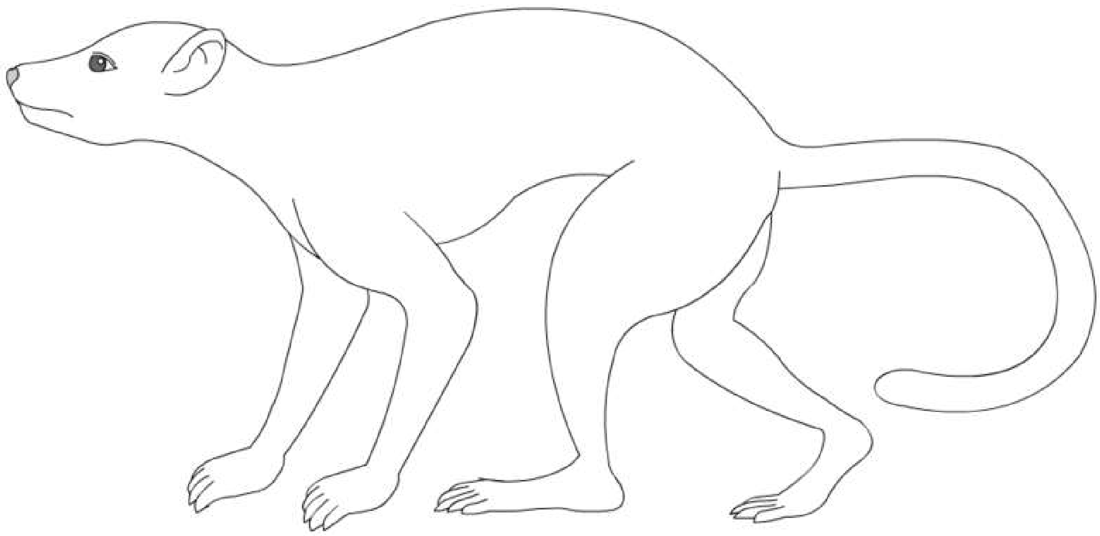
The first debates about the nature of human evolution arose between Thomas Huxley and Richard Owen. Huxley argued for human evolution from apes by illustrating many of the similarities and differences between humans and apes and did so particularly in his 1863 book *Evidence as to Man's Place in Nature*. However, many of Darwin's early supporters (such as Alfred Russel Wallace and Charles Lyell) did not agree that the origin of the mental capacities and the moral sensibilities of humans could be explained by natural selection. Darwin applied the theory of evolution and sexual selection to humans when he published *The Descent of Man* in 1871.

A major problem was the lack of fossil intermediaries. It was only in the 1920s that such fossils were discovered in Africa. In 1925, Raymond Dart described *Australopithecus africanus*. The type specimen was the Taung Child, an Australopithecine infant discovered in a cave. The child's remains were a remarkably well-preserved tiny skull and an endocranial cast of the individual's brain. Although the brain was small (410 cm^3), its shape was rounded, unlike that of chimpanzees and gorillas and more like a modern human brain. Also, the specimen showed short canine teeth and the position of the foramen magnum was evidence of bipedal locomotion. All of these traits convinced Dart that the Taung baby was a bipedal human ancestor, a transitional form between apes and humans.

The classification of humans and their relatives has changed considerably over time. The gracile Australopithecines are now thought to be ancestors of the genus *Homo*, the group to which modern humans belong. Both Australopithecines and *Homo sapiens* are part of the tribe Hominini. Recent data suggests Australopithecines were a diverse group and that *A. africanus* may not be a direct ancestor of modern humans. Reclassification of Australopithecines that originally were split into either gracile or robust varieties has put the latter into a family of its own, *Paranthropus*. Taxonomists place humans, Australopithecines and related species in the same family as other great apes, in the Hominidae.

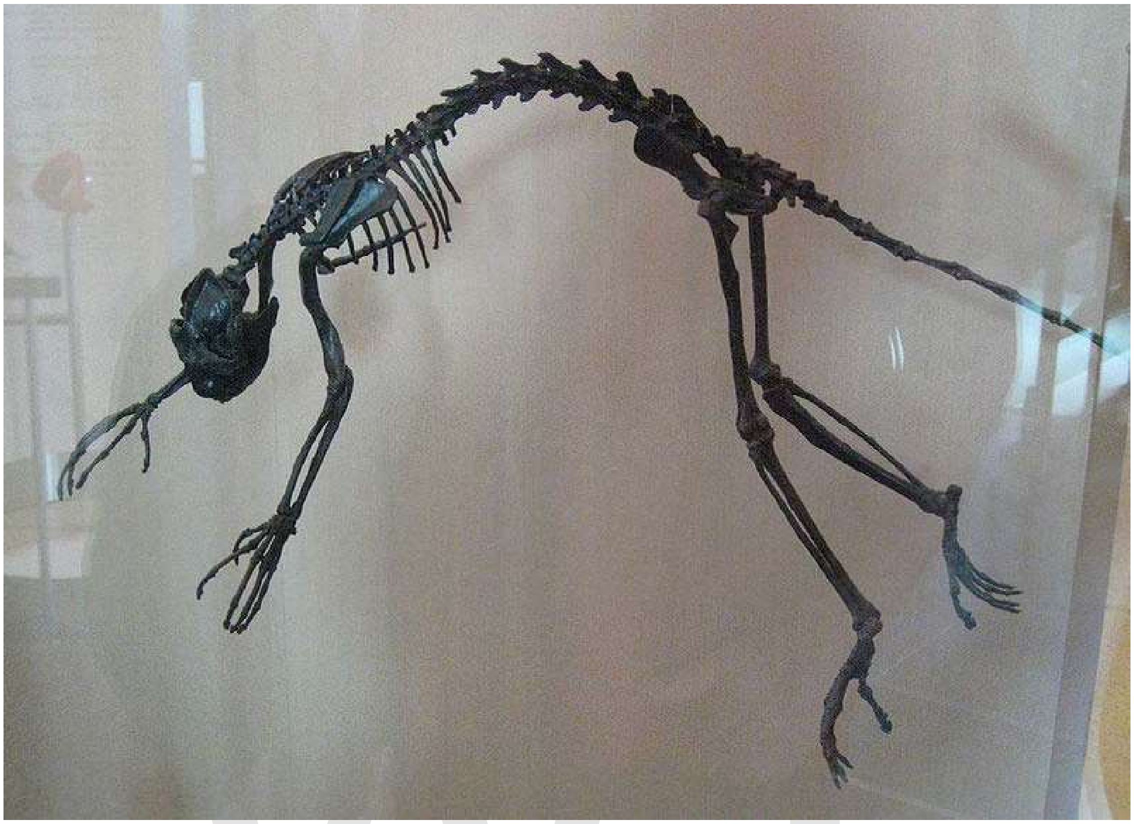
Note: 1e+06 years = 1 × 10^6 years = 1 million years ago = 1 Ma

Evolution of the great apes



Plesiadapis

The evolutionary history of the primates can be traced back 65 million years, as one of the oldest of all surviving placental mammal groups. The oldest known primate-like mammal species, the Plesiadapis, come from North America, but they were widespread in Eurasia and Africa during the tropical conditions of the Paleocene and Eocene.



Notharctus

The beginning of modern climates was marked by the formation of the first Antarctic ice in the early Oligocene around 30 million years ago. A primate from this time was *Notharctus*. Fossil evidence found in Germany in the 1980s was determined to be about 16.5 million years old, some 1.5 million years older than similar species from East Africa and challenging the original theory regarding human ancestry originating on the African continent.

David Begun says that these primates flourished in Eurasia and that the lineage leading to the African apes and humans— including Dryopithecus—migrated south from Europe or Western Asia into Africa. The surviving tropical population, which is seen most completely in the upper Eocene and lowermost Oligocene fossil beds of the Fayum depression southwest of Cairo, gave rise to all living primates—lemurs of Madagascar, lorises of Southeast Asia, galagos or "bush babies" of Africa and the anthropoids; platyrrhines or New World monkeys and catarrhines or Old World monkeys and the great apes and humans.

The earliest known catarrhine is *Kamoyapithecus* from uppermost Oligocene at Eragaleit in the northern Kenya Rift Valley, dated to 24 million years ago. Its ancestry is generally thought to be species related to *Aegyptopithecus*, *Propliopithecus* and *Parapithecus* from the Fayum, at around 35 million years ago. In 2010, *Saadanius* was described as a close relative of the last common ancestor of the crown catarrhines and tentatively dated to 29–28 million years ago, helping to fill an 11-million-year gap in the fossil record.

Reconstructed tailless *Proconsul* skeleton

In the early Miocene, about 22 million years ago, the many kinds of arboreally adapted primitive catarrhines from East Africa suggest a long history of prior diversification. Fossils at 20 million years ago include fragments attributed to *Victoriapithecus*, the earliest Old World Monkey. Among the genera thought to be in the ape lineage leading up to 13 million years ago are *Proconsul*, *Rangwapithecus*, *Dendropithecus*, *Limnopithecus*, *Nacholapithecus*, *Equatorius*, *Nyanzapithecus*, *Afropithecus*, *Heliopithecus* and *Kenyapithecus*, all from East Africa. The presence of other generalized non-cercopithecids of middle Miocene age from sites far distant—*Otavipithecus* from cave deposits in Namibia and *Pierolapithecus* and *Dryopithecus* from France, Spain and Austria—is evidence of a wide diversity of forms across Africa and the Mediterranean basin during the relatively warm and equable climatic regimes of the early and middle Miocene. The youngest of the Miocene hominoids, *Oreopithecus*, is from 9 million year old coal beds in Italy.

Molecular evidence indicates that the lineage of gibbons (family Hylobatidae) became distinct from Great Apes between 18 and 12 million years ago and that of orangutans (subfamily Ponginae) became distinct from the other Great Apes at about 12 million years; there are no fossils that clearly document the ancestry of gibbons, which may have originated in a so-far-unknown South East Asian hominoid population, but fossil proto-orangutans may be represented by *Ramapithecus* from India and *Griphopithecus* from Turkey, dated to around 10 million years ago.

Divergence of the human lineage from other Great Apes

Species close to the last common ancestor of gorillas, chimpanzees and humans may be represented by *Nakalipithecus* fossils found in Kenya and *Ouranopithecus* found in Greece. Molecular evidence suggests that between 8 and 4 million years ago, first the gorillas and then the chimpanzees (genus *Pan*) split off from the line leading to the humans; human DNA is approximately 98.4% identical to that of chimpanzees when comparing single nucleotide polymorphisms. The fossil record of gorillas and chimpanzees is quite limited. Both poor preservation (rain forest soils tend to be acidic and dissolve bone) and sampling bias probably contribute to this problem.

Other hominines likely adapted to the drier environments outside the equatorial belt, along with antelopes, hyenas, dogs, pigs, elephants and horses. The equatorial belt contracted after about 8 million years ago. Fossils of these hominans - the species in the human lineage following divergence from the chimpanzees - are relatively well known.

The earliest are *Sahelanthropus tchadensis* (7 Ma) and *Orrorin tugenensis* (6 Ma), followed by:

- *Ardipithecus* (5.5–4.4 Ma), with species *Ar. kadabba* and *Ar. ramidus*;
- *Australopithecus* (4–1.8 Ma), with species *Au. anamensis*, *Au. afarensis*, *Au. africanus*, *Au. bahrelghazali*, *Au. garhi* and *Au. sediba*;
- *Kenyanthropus* (3–2.7 Ma), with species *Kenyanthropus platyops*;
- *Paranthropus* (3–1.2 Ma), with species *P. aethiopicus*, *P. boisei* and *P. robustus*;
- *Homo* (2 Ma–present), with species *Homo habilis*, *Homo rudolfensis*, *Homo ergaster*, *Homo georgicus*, *Homo antecessor*, *Homo cepranensis*, *Homo erectus*, *Homo heidelbergensis*, *Homo rhodesiensis*, *Homo neanderthalensis*, *Homo sapiens idaltu*, *Archaic Homo sapiens*, *Homo floresiensis*.

Genus Homo

Homo sapiens is the only extant species of its genus, *Homo*. While some other, extinct, *Homo* species might have been ancestors of *Homo sapiens*, many were likely our "cousins", having speciated away from our ancestral line. There is not yet a consensus as to which of these groups should count as separate species and which as subspecies. In some cases this is due to the dearth of fossils, in other cases it is due to the slight differences used to classify species in the *Homo* genus. The Sahara pump theory (describing an occasionally passable "wet" Sahara Desert) provides an explanation of the early variation in the genus *Homo*.

Based on archaeological and paleontological evidence, it has been possible to infer, to some extent, the ancient dietary practices of various *Homo* species and to study the role of diet in physical and behavioral evolution within *Homo*.

H. habilis

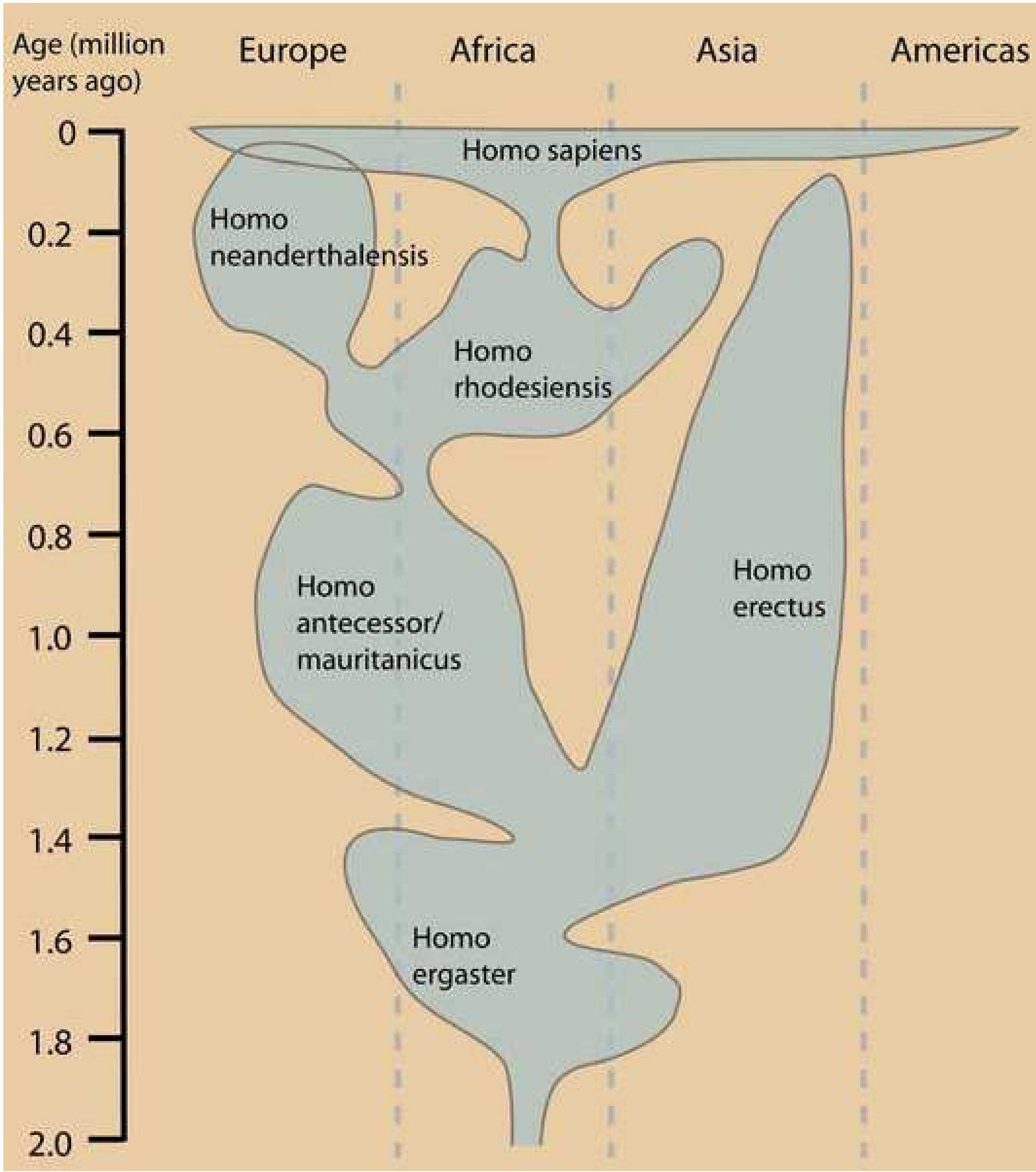
Homo habilis lived from about 2.4 to 1.4 Ma. *Homo habilis*, the first species of the genus *Homo*, evolved in South and East Africa in the late Pliocene or early Pleistocene, 2.5–2 Ma, when it diverged from the Australopithecines. *Homo habilis* had smaller molars and larger brains than the Australopithecines and made tools from stone and perhaps animal bones. One of the first known hominids, it was nicknamed 'handy man' by its discoverer, Louis Leakey due to its association with stone tools. Some scientists have proposed moving this species out of *Homo* and into *Australopithecus* due to the morphology of its skeleton being more adapted to living on trees rather than to moving on two legs like *Homo sapiens*.

H. rudolfensis and *H. georgicus*

These are proposed species names for fossils from about 1.9–1.6 Ma, the relation of which with *Homo habilis* is not yet clear.

- *Homo rudolfensis* refers to a single, incomplete skull from Kenya. Scientists have suggested that this was another *Homo habilis*, but this has not been confirmed.
- *Homo georgicus*, from Georgia, may be an intermediate form between *Homo habilis* and *Homo erectus*, or a sub-species of *Homo erectus*.

H. ergaster and *H. erectus*



One current view of the temporal and geographical distribution of hominid populations. Other interpretations differ mainly in the taxonomy and geographical distribution of hominid species.

The first fossils of *Homo erectus* were discovered by Dutch physician Eugene Dubois in 1891 on the Indonesian island of Java. He originally gave the material the name *Pithecanthropus erectus* based on its morphology that he considered to be intermediate between that of humans and apes. *Homo erectus* (H erectus) lived from about 1.8 Ma to about 70,000 years ago (which would indicate that they were probably wiped out by the Toba catastrophe; however, *Homo erectus soloensis* and *Homo floresiensis* survived it). Often the early phase, from 1.8 to 1.25 Ma, is considered to be a separate species, *Homo* *ergaster*, or it is seen as a subspecies of *Homo erectus*, *Homo erectus ergaster*. In the early Pleistocene, 1.5–1 Ma, in Africa, Asia and Europe, some populations of *Homo habilis* are thought to have evolved larger brains and made more elaborate stone tools; these differences and others are sufficient for anthropologists to classify them as a new species, *Homo erectus*. In addition *Homo erectus* was the first human ancestor to walk truly upright. This was made possible by the evolution of locking knees and a different location of the foramen magnum (the hole in the skull where the spine enters). They may have used fire to cook their meat.

A famous example of *Homo erectus* is Peking Man; others were found in Asia (notably in Indonesia), Africa and Europe. Many paleoanthropologists now use the term *Homo ergaster* for the non-Asian forms of this group and reserve *Homo erectus* only for those fossils that are found in Asia and meet certain skeletal and dental requirements which differ slightly from *H. ergaster*.

H. cepranensis and *H. antecessor*

These are proposed as species that may be intermediate between *H. erectus* and *H. heidelbergensis*.

- *H. antecessor* is known from fossils from Spain and England that are dated 1.2 Ma–500 ka.
- *H. cepranensis* refers to a single skull cap from Italy, estimated to be about 800,000 years old.

H. heidelbergensis

H. heidelbergensis (Heidelberg Man) lived from about 800,000 to about 300,000 years ago. Also proposed as *Homo sapiens heidelbergensis* or *Homo sapiens paleohungaricus*.

H. rhodesiensis and the Gawis cranium

- *H. rhodesiensis*, estimated to be 300,000–125,000 years old. Most current experts believe Rhodesian Man to be within the group of *Homo heidelbergensis*, though other designations such as Archaic Homo sapiens and Homo sapiens rhodesiensis have also been proposed.
- In February 2006 a fossil, the Gawis cranium, was found which might possibly be a species intermediate between *H. erectus* and *H. sapiens* or one of many evolutionary dead ends. The skull from Gawis, Ethiopia, is believed to be 500,000–250,000 years old. Only summary details are known and no peer reviewed studies have been released by the finding team. Gawis man's facial features suggest its being either an intermediate species or an example of a "Bodo man" female.

H. neanderthalensis

Le Ferrassie Neanderthal skull (cast)

H. neanderthalensis lived from 400,000 to about 30,000 years ago. Also proposed as *Homo sapiens neanderthalensis*. Evidence from sequencing mitochondrial DNA indicated that no significant gene flow occurred between *H. neanderthalensis* and *H. sapiens* and, therefore, the two were separate species that shared a common ancestor about 660,000 years ago. In 1997, Mark Stoneking stated: "These results [based on mitochondrial DNA extracted from Neanderthal bone] indicate that Neanderthals did not contribute mitochondrial DNA to modern humans… Neanderthals are not our ancestors". Subsequent investigation of a second source of Neanderthal DNA supported these findings.

However, the 2010 sequencing of the Neanderthal genome indicated that Neanderthals did indeed interbreed with *H. sapiens circa* 75,000 BC (after *H. sapiens* moved out from Africa, but before they separated into Europe, the Middle East and Asia). Nearly all modern humans have 1% to 4% of their DNA derived from Neanderthal DNA. This 1–4% bit of DNA is only present in non-African humans. However, supporters of the multiregional hypothesis point to recent studies indicating non-African nuclear DNA heritage dating to one Ma, although the reliability of these studies has been questioned. Competition from *Homo sapiens* probably contributed to Neanderthal extinction. They could have coexisted in Europe for as long as 10,000 years.

H. sapiens

H. sapiens (the adjective *sapiens* is Latin for "wise" or "intelligent") have lived from about 250,000 years ago to the present. Between 400,000 years ago and the second interglacial period in the Middle Pleistocene, around 250,000 years ago, the trend in skull expansion and the elaboration of stone tool technologies developed, providing evidence for a transition from *H. erectus* to *H. sapiens*. The direct evidence suggests there was a migration of *H. erectus* out of Africa, then a further speciation of *H. sapiens* from *H. erectus* in Africa. A subsequent migration within and out of Africa eventually replaced the earlier dispersed *H. erectus*. This migration and origin theory is usually referred to as the *recent single origin* or Out of Africa theory. Current evidence does not preclude some multiregional evolution or some admixture of the migrant *H. sapiens* with existing *Homo* populations. This is a hotly debated area of paleoanthropology.

Current research has established that humans are genetically highly homogenous; that is, the DNA of individuals is more alike than usual for most species, which may have resulted from their relatively recent evolution or the possibility of a population bottleneck resulting from cataclysmic natural events such as the Toba catastrophe. Distinctive genetic characteristics have arisen, however, primarily as the result of small groups of people moving into new environmental circumstances. These adapted traits are a very small component of the *Homo sapiens* genome, but include various characteristics such as skin color and nose form, in addition to internal characteristics such as the ability to breathe more efficiently at high altitudes.

H. sapiens idaltu, from Ethiopia, is an extinct sub-species who lived about 160,000 years ago.

H. floresiensis

H. floresiensis, which lived from approximately 100,000 to 12,000 before present, has been nicknamed *hobbit* for its small size, possibly a result of insular dwarfism. *H. floresiensis* is intriguing both for its size and its age, being a concrete example of a recent species of the genus *Homo* that exhibits derived traits not shared with modern humans. In other words, *H. floresiensis* share a common ancestor with modern humans, but split from the modern human lineage and followed a distinct evolutionary path. The main find was a skeleton believed to be a woman of about 30 years of age. Found in 2003 it has been dated to approximately 18,000 years old. The living woman was estimated to be one meter in height, with a brain volume of just 380 cm^3 (considered small for a chimpanzee and less than a third of the *H. sapiens* average of 1400 cm^3).

However, there is an ongoing debate over whether *H. floresiensis* is indeed a separate species. Some scientists presently believe that *H. floresiensis* was a modern *H. sapiens* suffering from pathological dwarfism. This hypothesis is supported in part, because some modern humans who live on Flores, the island where the skeleton was found, are pygmies. This coupled with pathological dwarfism, it is argued, could indeed create a hobbit-like human. The other major attack on *H. floresiensis* is that it was found with tools only associated with *H. sapiens*.

The hypothesis of pathological dwarfism, however, fails to explain additional anatomical features that are unlike those of modern humans (diseased or not) but much like those of ancient members of our genus. Aside from cranial features, these features include the form of bones in the wrist, forearm, shoulder, knees and feet.

Denisova hominin

In 2008, archaeologists working at the site of Denisova Cave in the Altai Mountains of Siberia uncovered a small bone fragment from the fifth finger of a juvenile hominin, dubbed the "X-woman" (referring to the maternal descent of mitochondrial DNA), or the Denisova hominin. Artifacts, including a bracelet, excavated in the cave at the same level were carbon dated to around 40,000 BP. As DNA had survived in the fossil fragment due to the cool climate of the Denisova Cave, a team of scientists from the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany sequenced mtDNA extracted from the fragment.

The analysis indicated that modern humans, Neanderthals and the Denisova hominin last shared a common ancestor around 1 million years ago. Modern humans are known to have overlapped with Neanderthals in Europe for more than 10,000 years and the discovery raises the possibility that Neanderthals, modern humans and the Denisovan hominin may have co-existed together.

The DNA analysis further indicated that this new hominin species was the result of an early migration out of Africa, distinct from the later out-of-Africa migrations associated with Neanderthals and modern humans, but also distinct from the earlier African exodus of *Homo erectus*. Professor Chris Stringer, human origins researcher at London's Natural History Museum and one of the leading proponents of the recent single-origin hypothesis, remarked: "This new DNA work provides an entirely new way of looking at the still poorly understood evolution of humans in central and eastern Asia." Pääbo noted that the existence of this distant branch creates a much more complex picture of humankind during the Late Pleistocene.

Comparative table of *Homo* species

Comparative table of *Homo* species

Species	Lived when (Ma)	Lived where	Adult height	Adult mass	Cranial capacity (cm³)	Fossil record	Discovery / publication of name
H. antecessor	1.2 – 0.8	Spain	1.75 m (5.7 ft)	90 kg (200 lb)	1,000	2 sites	1997
H. cepranensis	0.9 – 0.8?	Italy			1,000	1 skull cap	1994/2003
H. erectus	1.5 – 0.2	Africa, Eurasia (Java, China, India, Caucasus)	1.8 m (5.9 ft)	60 kg (130 lb)	850 (early) – 1,100 (late)	Many	1891/1892
H. ergaster	1.9 – 1.4	Eastern and Southern Africa	1.9 m (6.2 ft)		700–850	Many	1975
H. floresiensis	0.10? – 0.012	Indonesia	1.0 m (3.3 ft)	25 kg (55 lb)	400	7 individuals	2003/2004
H. gautengensis	>2 – 0.6	South Africa	1.0 m (3.3 ft)			1 individual	2010/2010
H. georgicus	1.8	Georgia			600	4 individuals	1999/2002
H. habilis	2.3 – 1.4	Africa	1.0–1.5 m (3.3–4.9 ft)	33–55 kg (73–120 lb)	510–660	Many	1960/1964
H. heidelbergensis	0.6 – 0.35	Europe, Africa, China	1.8 m (5.9 ft)	60 kg (130 lb)	1,100–1,400	Many	1908
H. neanderthalensis	0.35 – 0.03	Europe, Western Asia	1.6 m (5.2 ft)	55–70 kg (120–150 lb) (heavily built)	1,200–1,900	Many	(1829)/1864

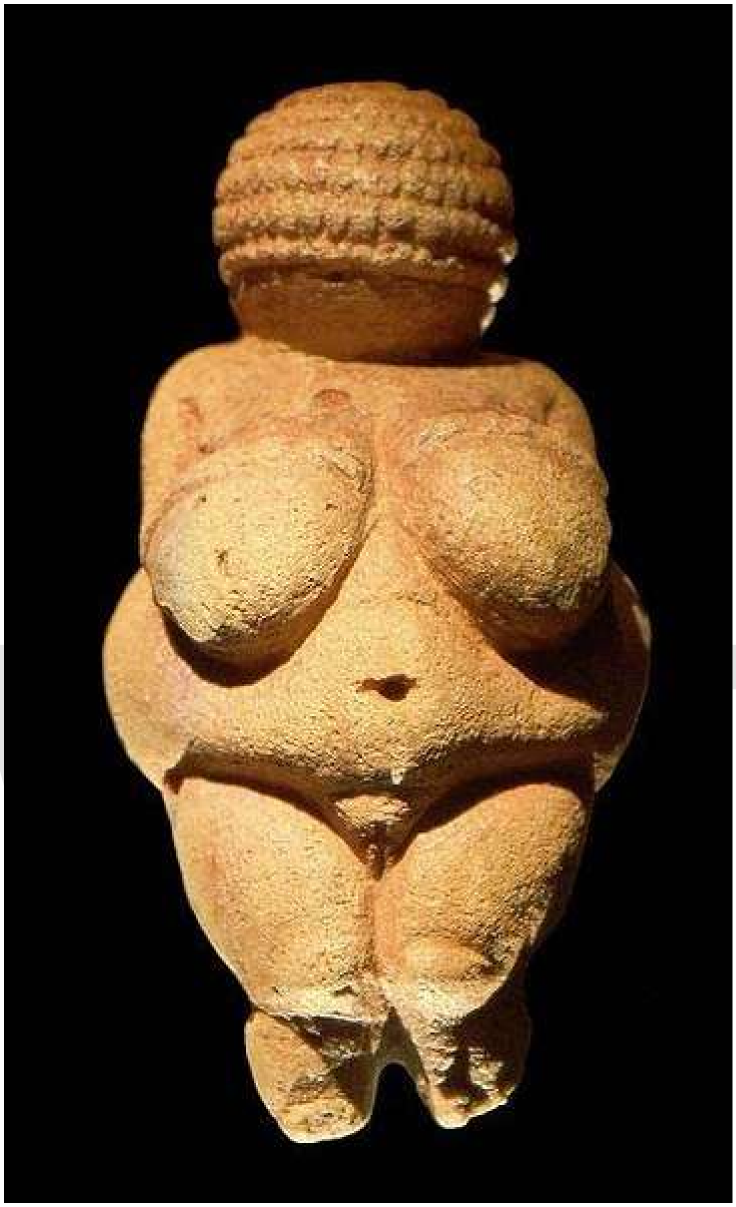
H. rhodesiensis	0.3 – 0.12	Zambia			1,300	Very few	1921
H. rudolfensis	1.9	Kenya				1 skull	1972/1986
H. sapiens idaltu	0.16 – 0.15	Ethiopia			1,450	3 craniums	1997/2003
H. sapiens sapiens (modern humans)	0.2 – present	Worldwide	1.4–1.9 m (4.6–6.2 ft)	50–100 kg (110–220 lb)	1,000–1,850	Still living	—/1758

Use of tools

"A sharp rock", an Oldowan pebble tool, the most basic of human stone tools

Fire, one of the greatest human discoveries

An Acheulean hand axe, the pinnacle of *Homo erectus* stone working



Venus of Willendorf, an example of Paleolithic art

Using tools has been interpreted as a sign of intelligence and it has been theorized that tool use may have stimulated certain aspects of human evolution—most notably the continued expansion of the human brain. Paleontology has yet to explain the expansion of this organ over millions of years despite being extremely demanding in terms of energy consumption. The brain of a modern human consumes about 20 watts (400 kilocalories per day), which is one fifth of the energy consumption of a human body. Increased tool use would allow hunting for energy-rich meat products and would enable processing more energy-rich plant products. Researchers have suggested that early hominids were thus under evolutionary pressure to increase their capacity to create and use tools.

Precisely when early humans started to use tools is difficult to determine, because the more primitive these tools are (for example, sharp-edged stones) the more difficult it is to decide whether they are natural objects or human artifacts. There is some evidence that the australopithecines (4 Ma) may have used broken bones as tools, but this is debated.

It should be noted that many species make and use tools, but it is the human species that dominates the areas of making and using more complex tools. The oldest known tools are the "Oldowan stone tools" from Ethiopia. It was discovered that these tools are from 2.5 to 2.6 million years old, which predates the earliest known "Homo" species. There is no known evidence that any "Homo" specimens appeared by 2.5 Ma. A Homo fossil was found near some Oldowan tools and its age was noted at 2.3 million years old, suggesting that maybe the Homo species did indeed create and use these tools. It is surely possible, but not solid evidence. Bernard Wood noted that "Paranthropus" coexisted with the early Homo species in the area of the "Oldowan Industrial Complex" over roughly the same span of time. Although there is no direct evidence that points to Paranthropus as the tool makers, their anatomy lends to indirect evidence of their capabilities in this area. Most paleoanthropologists agree that the early "Homo" species were indeed responsible for most of the Oldowan tools found. They argue that when most of the Oldowan tools were found in association with human fossils, Homo was always present, but Paranthropus was not.

In 1994, Randall Susman used the anatomy of opposable thumbs as the basis for his argument that both the Homo and Paranthropus species were toolmakers. He compared bones and muscles of human and chimpanzee thumbs, finding that humans have 3 muscles that chimps lack. Humans also have thicker metacarpals with broader heads, making the human hand more successful at precision grasping than the chimpanzee hand. Susman defended that modern anatomy of the human thumb is an evolutionary response to the requirements associated with making and handling tools and that both species were indeed toolmakers.

Stone tools

Stone tools are first attested around 2.6 Ma, when *H. habilis* in Eastern Africa used so-called pebble tools, choppers made out of round pebbles that had been split by simple strikes. This marks the beginning of the Paleolithic, or Old Stone Age; its end is taken to be the end of the last Ice Age, around 10,000 years ago. The Paleolithic is subdivided into the Lower Paleolithic (Early Stone Age, ending around 350,000–300,000 years ago), the Middle Paleolithic (Middle Stone Age, until 50,000–30,000 years ago) and the Upper Paleolithic.

The period from 700,000–300,000 years ago is also known as the Acheulean, when *H. ergaster* (or *erectus*) made large stone hand-axes out of flint and quartzite, at first quite rough (Early Acheulian), later "retouched" by additional, more subtle strikes at the sides of the flakes. After 350,000 BP (Before Present) the more refined so-called Levallois technique was developed. It consisted of a series of consecutive strikes, by which scrapers, slicers ("racloirs"), needles and flattened needles were made. Finally, after about

50,000 BP, ever more refined and specialized flint tools were made by the Neanderthals and the immigrant Cro-Magnons (knives, blades, skimmers). In this period they also started to make tools out of bone.

Modern humans and the "Great Leap Forward" debate

Until about 50,000–40,000 years ago the use of stone tools seems to have progressed stepwise. Each phase (*H. habilis*, *H. ergaster*, *H. neanderthalensis*) started at a higher level than the previous one, but once that phase started further development was slow. These *Homo* species were culturally conservative, but after 50,000 BC modern human culture started to change at a much greater speed. Jared Diamond, author of *The Third Chimpanzee* and some anthropologists characterize this as a "Great Leap Forward".

Modern humans started burying their dead, making clothing out of hides, developing sophisticated hunting techniques (such as using trapping pits or driving animals off cliffs) and engaging in cave painting. As human culture advanced, different populations of humans introduced novelty to existing technologies: artifacts such as fish hooks, buttons and bone needles show signs of variation among different populations of humans, something that had not been seen in human cultures prior to 50,000 BP. Typically, *H. neanderthalensis* populations do not vary in their technologies.

Among concrete examples of Modern human behavior, anthropologists include specialization of tools, use of jewellery and images (such as cave drawings), organization of living space, rituals (for example, burials with grave gifts), specialized hunting techniques, exploration of less hospitable geographical areas and barter trade networks. Debate continues as to whether a "revolution" led to modern humans ("the big bang of human consciousness"), or whether the evolution was more gradual.

Models of human evolution

Today, all humans belong to one population of *Homo sapiens sapiens,* undivided by species barrier. However, according to the "Out of Africa" model this is not the first species of hominids: the first species of genus *Homo*, *Homo habilis*, evolved in East Africa at least 2 Ma and members of this species populated different parts of Africa in a relatively short time. *Homo erectus* evolved more than 1.8 Ma and by 1.5 Ma had spread throughout the Old World.

Anthropologists have been divided as to whether current human population evolved as one interconnected population (as postulated by the Multiregional Evolution hypothesis), or evolved only in East Africa, speciated, then migrated out of Africa and replaced human populations in Eurasia (called the "Out of Africa" Model or the "Complete Replacement" Model).

Multiregional model

Multiregional evolution, a *model to account for the pattern of human evolution*, was proposed by Milford H. Wolpoff in 1988. Multiregional evolution holds that human evolution from the beginning of the Pleistocene 2.5 million years BP to the present day has been within a single, continuous human species, evolving worldwide to modern *Homo sapiens*.

According to the multiregional hypothesis, fossil and genomic data are evidence for worldwide human evolution and contradict the recent speciation postulated by the Recent African origin hypothesis. The fossil evidence was insufficient for Richard Leakey to resolve this debate. Studies of haplogroups in Y-chromosomal DNA and mitochondrial DNA have largely supported a recent African origin. Evidence from autosomal DNA also supports the Recent African origin. However the presence of archaic admixture in modern humans remains a possibility and has been suggested by some studies.

Out of Africa

According to the Out of Africa model, developed by Chris Stringer and Peter Andrews, modern *H. sapiens* evolved in Africa 200,000 years ago. *Homo sapiens* began migrating from Africa between 70,000 – 50,000 years ago and eventually replaced existing hominid species in Europe and Asia. Out of Africa has gained support from research using mitochondrial DNA (mtDNA). After analysing genealogy trees constructed using 133 types of mtDNA, researchers concluded that all were descended from a woman from Africa, dubbed Mitochondrial Eve. Out of Africa is also supported by the fact that mitochondrial genetic diversity is highest among African populations.

There are differing theories on whether there was a single exodus or several. A multiple dispersal model involves the Southern Dispersal theory, which has gained support in recent years from genetic, linguistic and archaeological evidence. In this theory, there was a coastal dispersal of modern humans from the Horn of Africa around 70,000 years ago. This group helped to populate Southeast Asia and Oceania, explaining the discovery of early human sites in these areas much earlier than those in the Levant. A second wave of humans dispersed across the Sinai peninsula into Asia, resulting in the bulk of human population for Eurasia. This second group possessed a more sophisticated tool technology and was less dependent on coastal food sources than the original group. Much of the evidence for the first group's expansion would have been destroyed by the rising sea levels at the end of the Holocene era. The multiple dispersal model is contradicted by studies indicating that the populations of Eurasia and the populations of Southeast Asia and Oceania are all descended from the same mitochondrial DNA lineages, which support a single migration out of Africa that gave rise to all non-African populations.

The broad study of African genetic diversity headed by Dr. Sarah Tishkoff found the San people to express the greatest genetic diversity among the 113 distinct populations sampled, making them one of 14 "ancestral population clusters". The research also located the origin of modern human migration in south-western Africa, near the coastal border of Namibia and Angola.

According to the Toba catastrophe theory to which some anthropologists and archeologists subscribe, the supereruption of Lake Toba on Sumatra island in Indonesia roughly 70,000 years ago had global consequences, killing most humans then alive and creating a population bottleneck that affected the genetic inheritance of all humans today.

Recent and current human evolution

Natural selection is being observed in contemporary human populations, with recent findings demonstrating the population which is at risk of the severe debilitating disease kuru has significant over-representation of an immune variant of the prion protein gene G127V versus non-immune alleles. Scientists postulate one of the reasons for the rapid selection of this genetic variant is the lethality of the disease in non-immune persons. Other reported evolutionary trends in other populations include a lengthening of the reproductive period, reduction in cholesterol levels, blood glucose and blood pressure.

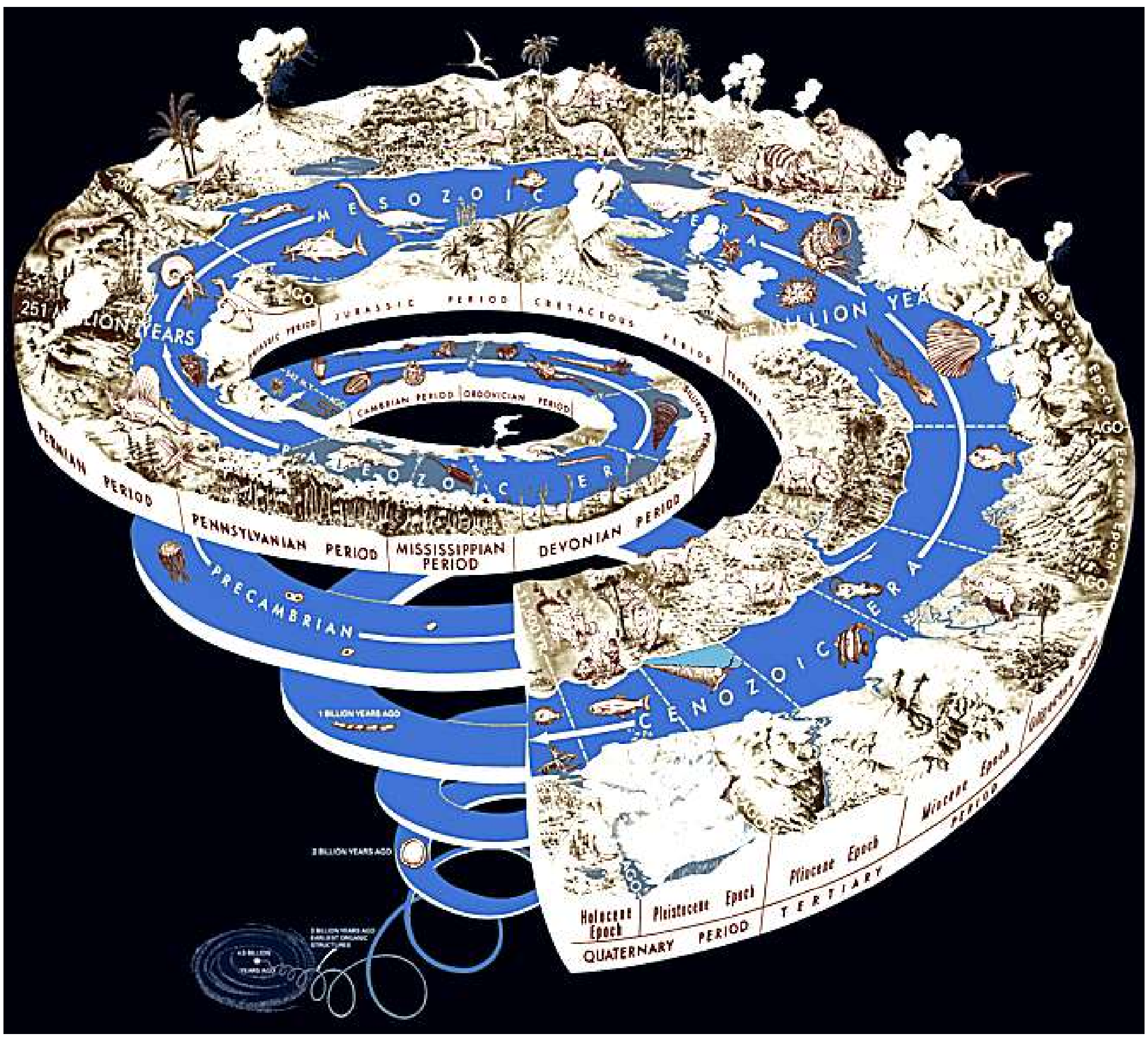
In their 2009 book *The 10,000 Year Explosion*, Gregory Cochran and Henry Harpending argue that human evolution has accelerated since and as a result of the development of agriculture and civilisation since some 50,000 years ago and that there are consequently substantial genetic differences between different current human populations.

Genetics

Human evolutionary genetics studies how one human genome differs from the other, the evolutionary past that gave rise to it and its current effects. Differences between genomes have anthropological, medical and forensic implications and applications. Genetic data can provide important insight into human evolution.

Chapter- 2

Paleontology



Paleontology investigates the entire history of life on Earth

A paleontologist at work at John Day Fossil Beds National Monument

The preparation of the fossilized bones of *Europasaurus holgeri*

Paleontology (British: **palaeontology**) is the study of prehistoric life, including organisms' evolution and interactions with each other and their environments (their paleoecology). As a "historical science" it tries to explain causes rather than conduct experiments to observe effects. Paleontological observations have been documented as far back as the 5th century BC. The science became established in the 18th century as a result of Georges Cuvier's work on comparative anatomy and developed rapidly in the 19th century. Fossils found in China since the 1990s have provided new information about the earliest evolution of animals, early fish, dinosaurs and the evolution of birds and mammals. Paleontology lies on the border between biology and geology and shares with archaeology a border that is difficult to define. It now uses techniques drawn from a wide range of sciences, including biochemistry, mathematics and engineering. As knowledge has increased, paleontology has developed specialized subdivisions, some of which focus on different types of fossil organisms while others study ecological and environmental history, such as ancient climates.

Body fossils and trace fossils are the principal types of evidence about ancient life and geochemical evidence has helped to decipher the evolution of life before there were organisms large enough to leave fossils. Estimating the dates of these remains is essential but difficult: sometimes adjacent rock layers allow radiometric dating, which provides absolute dates that are accurate to within 0.5%, but more often paleontologists have to rely on relative dating by solving the "jigsaw puzzles" of biostratigraphy. Classifying ancient organisms is also difficult, as many do not fit well into the Linnean taxonomy that is commonly used for classifying living organisms and paleontologists more often use cladistics to draw up evolutionary "family trees". The final quarter of the 20th century saw the development of molecular phylogenetics, which investigates how closely organisms are related by measuring how similar the DNA is in their genomes. Molecular phylogenetics has also been used to estimate the dates when species diverged, but there is controversy about the reliability of the molecular clock on which such estimates depend.

Use of all these techniques has enabled paleontologists to discover much of the evolutionary history of life, almost all the way back to when Earth became capable of supporting life, about 3,800 million years ago. For about half of that time the only life was single-celled micro-organisms, mostly in microbial mats that formed ecosystems only a few millimeters thick. Earth's atmosphere originally contained virtually no oxygen and its oxygenation began about 2,400 million years ago. This may have caused an accelerating increase in the diversity and complexity of life and early multicellular plants and fungi have been found in rocks dated from 1,700 to 1,200 million years ago. The earliest multicellular animal fossils are much later, from about 580 million years ago, but animals diversified very rapidly and there is a lively debate about whether most of this happened in a relatively short Cambrian explosion or started earlier but has been hidden by lack of fossils. All of these organisms lived in water, but plants and invertebrates started colonizing land from about 490 million years ago and vertebrates followed them about 370 million years ago. The first dinosaurs appeared about 230 million years ago and birds evolved from one dinosaur group about 150 million years ago. During the time of the dinosaurs, mammals' ancestors survived only as small, mainly nocturnal insectivores, but after the non-avian dinosaurs became extinct in the Cretaceous–Tertiary extinction event 65 million years ago mammals diversified rapidly. Flowering plants appeared and rapidly diversified between 130 million years ago and 90 million years ago, possibly helped by coevolution with pollinating insects. Social insects appeared around the same time and, although they have relatively few species, now form over 50% of the total mass of all insects. Humans evolved from a lineage of upright-walking apes whose earliest fossils date from over 6 million years ago and anatomically modern humans appeared under 200,000 years ago. The course of evolution has been changed several times by mass extinctions that wiped out previously dominant groups and allowed other to rise from obscurity to become major components of ecosystems.

Definition

A paleontologist carefully chips rock from a column of dinosaur vertebrae

The simplest definition is "the study of ancient life". Paleontology seeks information about several aspects of past organisms: "their identity and origin, their environment and evolution and what they can tell us about the Earth's organic and inorganic past".

A historical science

Paleontology is one of the historical sciences, along with archaeology, geology, biology, astronomy, cosmology, philology and history itself. This means that it aims to describe phenomena of the past and reconstruct their causes. Hence it has three main elements: description of the phenomena; developing a general theory about the causes of various types of change; and applying those theories to specific facts.

When trying to explain past phenomena, paleontologists and other historical scientists often construct a set of hypotheses about the causes and then look for a "smoking gun", a piece of evidence which indicates that one of the hypotheses is a better explanation than the others. Sometimes the "smoking gun" is discovered by a fortunate accident during other research, for example the discovery by Luis Alvarez and Walter Alvarez of an iridium-rich layer at the Cretaceous–Tertiary boundary made asteroid impact and volcanism the most favored explanations for the Cretaceous–Tertiary extinction event.

The other main type of science is experimental science, which is often said to work by conducting experiments to *disprove* hypotheses about the workings and causes of natural phenomena – note that this approach cannot prove a hypothesis is correct, since some later experiment may disprove it. However, when confronted with totally unexpected phenomena, such as the first evidence for invisible radiation, experimental scientists often use the same approach as historical scientists: construct a set of hypotheses about the causes and then look for a "smoking gun".

Related sciences

Paleontology lies on the boundary between biology and geology since paleontology focuses on the record of past life but its main source of evidence is fossils, which are found in rocks. For historical reasons paleontology is part of the geology departments of many universities, because in the 19th century and early 20th century geology departments found paleontological evidence important for estimating the ages of rocks while biology departments showed little interest.

Paleontology also has some overlap with archaeology, which primarily works with objects made by humans and with human remains, while paleontologists are interested in the characteristics and evolution of humans as organisms. When dealing with evidence about humans, archaeologists and paleontologists may work together – for example paleontologists might identify animal or plant fossils around an archaeological site, to discover what the people who lived there ate; or they might analyze the climate at the time when the site was inhabited by humans.

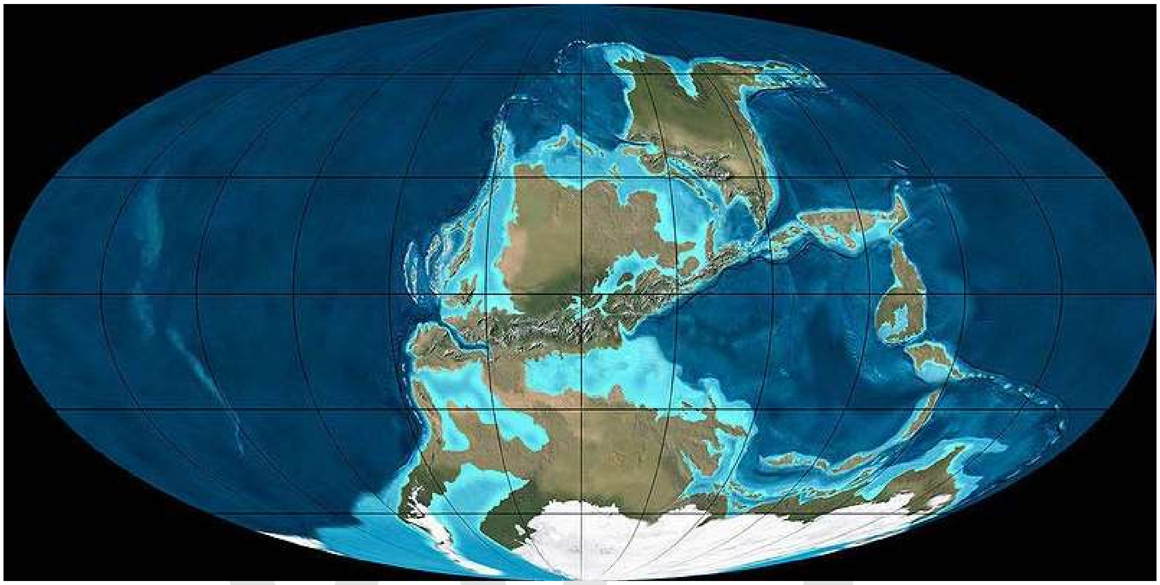
Analyses using engineering techniques show that *Tyrannosaurus* had a devastating bite, but raise doubts about how fast it could move.

In addition paleontology often uses techniques derived from other sciences, including biology, ecology, chemistry, physics and mathematics. For example geochemical signatures from rocks may help to discover when life first arose on Earth and analyses of carbon isotope ratios may help to identify climate changes and even to explain major transitions such as the Permian–Triassic extinction event. A relatively recent discipline, molecular phylogenetics, often helps by using comparisons of different modern organisms' DNA and RNA to re-construct evolutionary "family trees"; it has also been used to estimate the dates of important evolutionary developments, although this approach is controversial because of doubts about the reliability of the "molecular clock". Techniques developed in engineering have been used to analyse how ancient organisms might have worked, for example how fast *Tyrannosaurus* could move and how powerful its bite was.

Paleontology even contributes to astrobiology, the investigation of possible life on other planets, by developing models of how life may have arisen and by providing techniques for detecting evidence of life.

Subdivisions

As knowledge has increased, paleontology has developed specialised subdivisons. Vertebrate paleontology concentrates on fossils of vertebrates, from the earliest fish to the immediate ancestors of modern mammals. Invertebrate paleontology deals with fossils of invertebrates such as molluscs, arthropods, annelid worms and echinoderms. Paleobotany focuses on the study of fossil plants, but traditionally includes the study of fossil algae and fungi. Palynology, the study of pollen and spores produced by land plants and protists, straddles the border between paleontology and botany, as it deals with both living and fossil organisms. Micropaleontology deals with all microscopic fossil organisms, regardless of the group to which they belong.



In the Carboniferous period, the continents were not in the same places as they are today and there was extensive glaciation.

Instead of focusing on individual organisms, paleoecology examines the interactions between different organisms, such as their places in food chains and the two-way interaction between organisms and their environment – for example the development of oxygenic photosynthesis by bacteria hugely increased the productivity and diversity of ecosystems and also caused the oxygenation of the atmosphere, which in turn was a prerequisite for the evolution of the most complex eucaryotic cells, from which all multicellular organisms are built. Paleoclimatology, although sometimes treated as part of paleoecology, focuses more on the history of Earth's climate and the mechanisms which have changed it – which have sometimes included evolutionary developments, for example the rapid expansion of land plants in the Devonian period removed more carbon dioxide from the atmosphere, reducing the greenhouse effect and thus helping to cause an ice age in the Carboniferous period.

Biostratigraphy, the use of fossils to work out the chronological order in which rocks were formed, is useful to both paleontologists and geologists. Biogeography studies the spatial distribution of organisms and is also linked to geology, which explains how Earth's geography has changed over time.

Sources of evidence

Body fossils

This *Marrella* specimen illustrates how clear and detailed the fossils from the Burgess Shale lagerstätte are.

Fossils of organisms' bodies are usually the most informative type of evidence. The most common types are wood, bones and shells. Fossilisation is a rare event and most fossils are destroyed by erosion or metamorphism before they can be observed. Hence the fossil record is very incomplete, increasingly so further back in time. Despite this, it is often adequate to illustrate the broader patterns of life's history. There are also biases in the fossil record: different environments are more favorable to the preservation of different types of organism or parts of organisms. Further, only the parts of organisms that were already mineralised are usually preserved, such as the shells of molluscs. Since most animal species are soft-bodied, they decay before they can become fossilised. As a result, although there are 30-plus phyla of living animals, two-thirds have never been found as fossils.

Occasionally, unusual environments may preserve soft tissues. These lagerstätten allow paleontologists to examine the internal anatomy of animals that in other sediments are represented only by shells, spines, claws, etc. – if they are preserved at all. However, even lagerstätten present an incomplete picture of life at the time. The majority of organisms living at the time are probably not represented because lagerstätten are restricted to a narrow range of environments, e.g. where soft-bodied organisms can be preserved very quickly by events such as mudslides; and the exceptional events that cause quick burial make it difficult to study the normal environments of the animals. The sparseness of the fossil record means that organisms are expected to exist long before and after they are found in the fossil record – this is known as the Signor-Lipps effect.

Trace fossils

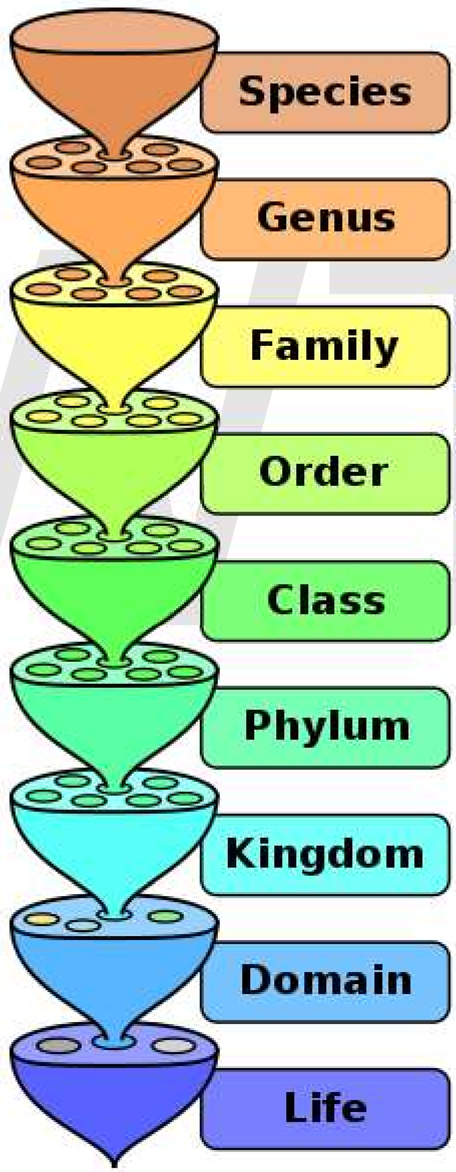
Cambrian trace fossils including *Rusophycus*, made by a trilobite

Trace fossils consist mainly of tracks and burrows, but also include coprolites (fossil feces) and marks left by feeding. Trace fossils are particularly significant because they represent a data source that is not limited to animals with easily-fossilized hard parts and which reflects organisms' behaviour. Also many traces date from significantly earlier than the body fossils of animals that are thought to have been capable of making them. Whilst exact assignment of trace fossils to their makers is generally impossible, traces may for example provide the earliest physical evidence of the appearance of moderately complex animals (comparable to earthworms).

Geochemical observations

Geochemical observations may help to deduce the global level of biological activity, or the affinity of a certain fossil. For example geochemical features of rocks may reveal when life first arose on Earth and may provide evidence of the presence of eucaryotic cells, the type from which all multicellular organisms are built. Analyses of carbon isotope ratios may help to explain major transitions such as the Permian–Triassic extinction event.

Classifying ancient organisms



Levels in the Linnean taxonomy

Naming groups of organisms in a way that is clear and widely agreed is important, as some disputes in palaeontology have been based just on misunderstandings over names. Linnean taxonomy is commonly used for classifying living organisms, but runs into difficulties when dealing with newly-discovered organisms that are significantly different from known ones. For example: it is hard to decide at what level to place a new higher-level grouping, e.g. genus or family or order; this is important since the Linnean rules for naming groups are tied to their levels and hence if a group is moved to a different level it has to be renamed.

Paleontologists generally use approaches based on cladistics, a technique for working out the evolutionary "family tree" of a set of organisms. It works by the logic that, if groups B and C have more similarities to each other than either has to group A, then B and C are more closely related to each other than either is to A. Characters that are compared may be anatomical, such as the presence of a notochord, or molecular, by comparing sequences of DNA or proteins. The result of a successful analysis is a hierarchy of clades – groups that share a common ancestor. Ideally the "family tree" has only two branches leading from each node ("junction"), but sometimes there is too little information to achieve this and paleontologists have to make do with junctions that have several branches. The cladistic technique is sometimes fallible, as some features, such as wings or camera eyes, evolved more than once, convergently – this must be taken into account in analyses.

Evolutionary developmental biology, commonly abbreviated to "Evo Devo", also helps paleontologists to produce "family trees". For example the embryological development of some modern brachiopods suggests that brachiopods may be descendants of the halkieriids, which became extinct in the Cambrian period.

Estimating the dates of organisms

Paleontology seeks to map out how living things have changed through time. A substantial hurdle to this aim is the difficulty of working out how old fossils are. Beds which preserve fossils typically lack the radioactive elements needed for radiometric dating. This technique is our only means of giving rocks greater than about 50 million years old an absolute age and can be accurate to within 0.5% or better. Although radiometric dating requires very careful laboratory work, its basic principle is simple: the rates at which various radioactive elements decay are known and so the ratio of the radioactive element to the element into which it decays shows how long ago the radioactive element was incorporated into the rock. Radioactive elements are common only in rocks with a volcanic origin and so the only fossil-bearing rocks that can be dated radiometrically are a few volcanic ash layers.

Consequently, paleontologists must usually rely on stratigraphy to date fossils. Stratigraphy is the science of deciphering the "layer-cake" that is the sedimentary record and has been compared to a jigsaw puzzle. Rocks normally form relatively horizontal layers, with each layer younger than the one underneath it. If a fossil is found between two layers whose ages are known, the fossil's age must lie between the two known ages. Because rock sequences are not continuous, but may be broken up by faults or periods of erosion, it is very difficult to match up rock beds that are not directly next to one another. However, fossils of species that survived for a relatively short time can be used to link up isolated rocks: this technique is called *biostratigraphy*. For instance, the conodont *Eoplacognathus pseudoplanus* has a short range in the Middle Ordovician period. If rocks of unknown age are found to have traces of *E. pseudoplanus*, they must have a mid-Ordovician age. Such index fossils must be distinctive, be globally distributed and have a short time range to be useful. However, misleading results are produced if the index fossils turn out to have longer fossil ranges than first thought. Stratigraphy and biostratigraphy can in general provide only relative dating (*A* was before *B*), which is often sufficient for studying evolution. However, this is difficult for some time periods, because of the problems involved in matching up rocks of the same age across different continents.

Family-tree relationships may also help to narrow down the date when lineages first appeared. For instance, if fossils of B or C date to X million years ago and the calculated "family tree" says A was an ancestor of B and C, then A must have evolved more than X million years ago.

It is also possible to estimate how long ago two living clades diverged – i.e. approximately how long ago their last common ancestor must have lived – by assuming that DNA mutations accumulate at a constant rate. These "molecular clocks", however, are fallible and provide only a very approximate timing: for example, they are not sufficiently precise and reliable for estimating when the groups that feature in the Cambrian explosion first evolved and estimates produced by different techniques may vary by a factor of two.

Overview of the history of life

The evolutionary history of life stretches back to over 3,000 million years ago, possibly as far as 3,800 million years ago. Earth formed about 4,540 million years ago and, after a collision that formed the Moon about 40 million years later, may have cooled quickly enough to have oceans and an atmosphere about 4,440 million years ago. However there is evidence on the Moon of a Late Heavy Bombardment from 4,000 to 3,800 million years ago. If, as seem likely, such a bombardment struck Earth at the same time, the first atmosphere and oceans may have been stripped away. The oldest clear evidence of life on Earth dates to 3,000 million years ago, although there have been reports, often disputed, of fossil bacteria from 3,400 million years ago and of geochemical evidence for the presence of life 3,800 million years ago. Even the simplest modern organisms are too complex to have emerged directly from non-living materials. Some scientists have proposed that life on Earth was "seeded" from elsewhere, but most research concentrates on various explanations of how life could have arisen independently on Earth.

This wrinkled "elephant skin" texture is a trace fossil of a non-stromatolite microbial mat. The image shows the location, in the Burgsvik beds of Sweden, where the texture was first identified as evidence of a microbial mat.

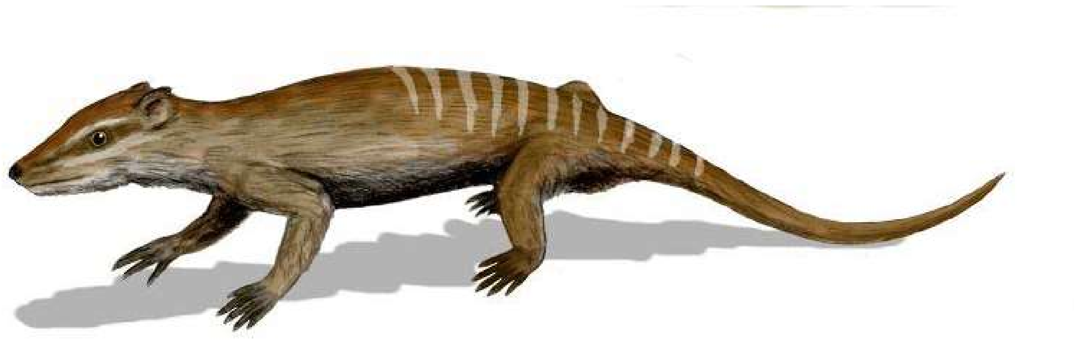
For about 2,000 million years microbial mats, multi-layered colonies of different types of bacteria, were the dominant life on Earth. The evolution of oxygenic photosynthesis enabled them to play the major role in the oxygenation of the atmosphere from about 2,400 million years ago. This change in the atmosphere increased their effectiveness as nurseries of evolution. While eukaryotes, cells with complex internal structures, may have been present earlier, their evolution speeded up when they acquired the ability to transform oxygen from a poison to a powerful source of energy in their metabolism. This innovation may have come from primitive eukaryotes capturing oxygen-powered bacteria as endosymbionts and transforming them into organelles called mitochondria. The earliest evidence of complex eukaryotes with organelles such as mitochondria, dates from 1,850 million years ago.

Multicellular life is composed only of eukaryotic cells and the earliest evidence for it is the Francevillian Group Fossils from 2,100 million years ago, although specialization of cells for different functions first appears between 1,430 million years ago (a possible fungus) and 1,200 million years ago (a probable red alga). Sexual reproduction may be a prerequisite for specialization of cells, as an asexual multicellular organism might be at risk of being taken over by rogue cells that retain the ability to reproduce.

Opabinia made the largest single contribution to modern interest in the Cambrian explosion.

The earliest known animals are cnidarians from about 580 million years ago, but these are so modern-looking that the earliest animals must have appeared before then. Early fossils of animals are rare because they did not develop mineralized hard parts that fossilize easily until about 548 million years ago. The earliest modern-looking bilaterian animals appear in the Early Cambrian, along with several "weird wonders" that bear little obvious resemblance to any modern animals. There is a long-running debate about whether this Cambrian explosion was truly a very rapid period of evolutionary experimentation; alternative views are that modern-looking animals began evolving earlier but fossils of their precursors have not yet been found, or that the "weird wonders" are evolutionary "aunts" and "cousins" of modern groups. Vertebrates remained an obscure group until the first fish with jaws appeared in the Late Ordovician.

The spread of life from water to land required organisms to solve several problems, including protection against drying out and supporting themselves against gravity. The earliest evidence of land plants and land invertebrates date back to about 476 million years ago and 490 million years ago respectively. The lineage that produced land vertebrates evolved later but very rapidly between 370 million years ago and 360 million years ago; recent discoveries have overturned earlier ideas about the history and driving forces behind their evolution. Land plants were so successful that they caused an ecological crisis in the Late Devonian, until the evolution and spread of fungi that could digest dead wood.



At about 13 centimetres (5.1 in) the Early Cretaceous *Yanoconodon* was longer than the average mammal of the time.

Birds are the last surviving dinosaurs

During the Permian period synapsids, including the ancestors of mammals, may have dominated land environments, but the Permian–Triassic extinction event 251 million years ago came very close to wiping out complex life. During the slow recovery from this catastrophe a previously obscure group, archosaurs, became the most abundant and diverse terrestrial vertebrates. One archosaur group, the dinosaurs, were the dominant land vertebrates for the rest of the Mesozoic and birds evolved from one group of dinosaurs. During this time mammals' ancestors survived only as small, mainly nocturnal insectivores, but this apparent set-back may have accelerated the development of mammalian traits such as endothermy and hair. After the Cretaceous–Tertiary extinction event 65 million years ago killed off the non-avian dinosaurs – birds are the only surviving dinosaurs – mammals increased rapidly in size and diversity and some took to the air and the sea.

A modern social insect collects pollen from a modern flowering plant

Fossil evidence indicates that flowering plants appeared and rapidly diversified in the Early Cretaceous, between 130 million years ago and 90 million years ago. Their rapid rise to dominance of terrestrial ecosystems is thought to have been propelled by coevolution with pollinating insects. Social insects appeared around the same time and, although they account for only small parts of the insect "family tree", now form over 50% of the total mass of all insects.

Humans evolved from a lineage of upright-walking apes whose earliest fossils date from over 6 million years ago. Although early members of this lineage had chimp-sized brains, about 25% as big as modern humans', there are signs of a steady increase in brain size after about 3 million years ago. There is a long-running debate about whether *modern* humans are descendants of a single small population in Africa, which then migrated all over the world less than 200,000 years ago and replaced previous hominine species, or arose worldwide at the same time as a result of interbreeding.

Mass extinctions

Life on earth has suffered occasional mass extinctions at least since 542 million years ago. Although they are disasters at the time, mass extinctions have sometimes accelerated the evolution of life on earth. When dominance of particular ecological niches passes from one group of organisms to another, it is rarely because the new dominant group is "superior" to the old and usually because an extinction event eliminates the old dominant group and makes way for the new one.

The fossil record appears to show that the rate of extinction is slowing down, with both the gaps between mass extinctions becoming longer and the average and background rates of extinction decreasing. However, it is not certain whether the actual rate of extinction has altered, since both of these observations could be explained in several ways:

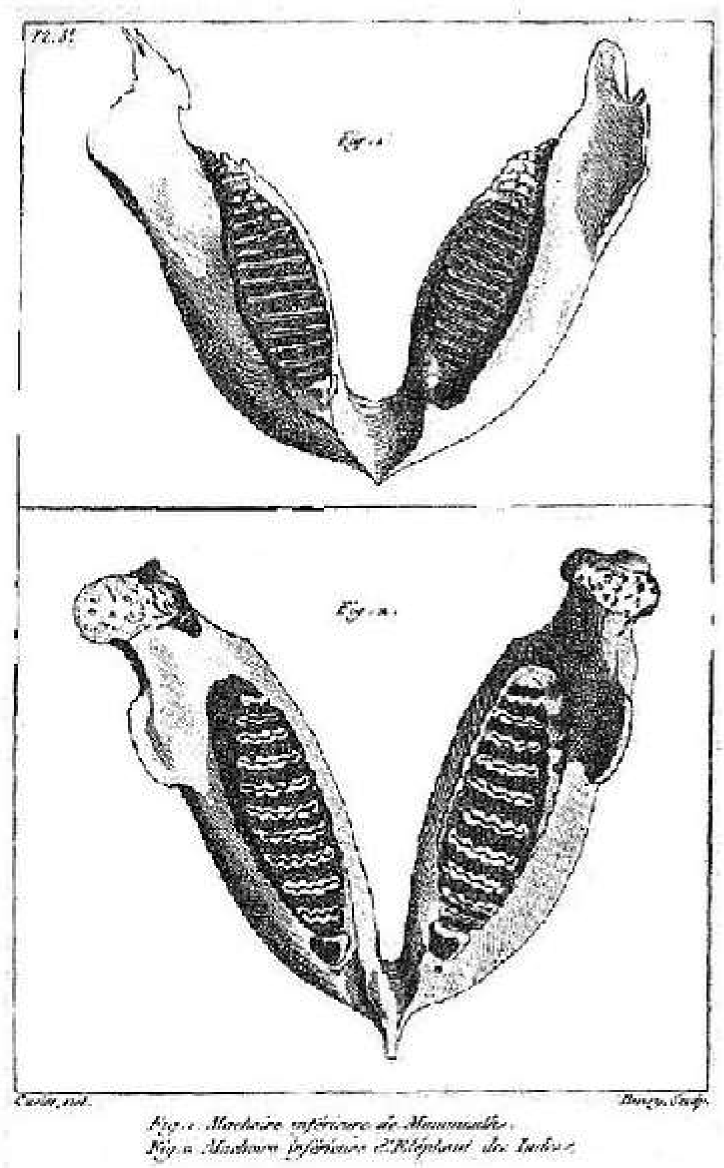
- The oceans may have become more hospitable to life over the last 500 million years and less vulnerable to mass extinctions: dissolved oxygen became more widespread and penetrated to greater depths; the development of life on land reduced the run-off of nutrients and hence the risk of eutrophication and anoxic events; marine ecosystems became more diversified so that food chains were less likely to be disrupted.

- Reasonably complete fossils are very rare, most extinct organisms are represented only by partial fossils and complete fossils are rarest in the oldest rocks. So paleontologists have mistakenly assigned parts of the same organism to different genera which were often defined solely to accommodate these finds – the story of *Anomalocaris* is an example of this. The risk of this mistake is higher for older fossils because these are often unlike parts of any living organism. Many of the "superfluous" genera are represented by fragments which are not found again and the "superfluous" genera appear to become extinct very quickly.

Biodiversity in the fossil record, which is

> "the number of distinct genera alive at any given time; that is, those whose first occurrence predates and whose last occurrence postdates that time"

shows a different trend: a fairly swift rise from 542 to 400 million years ago, a slight decline from 400 to 200 million years ago, in which the devastating Permian–Triassic extinction event is an important factor and a swift rise from 200 million years ago to the present.



This illustration of an Indian elephant jaw and a mammoth jaw (top) is from Cuvier's 1796 paper on living and fossil elephants.

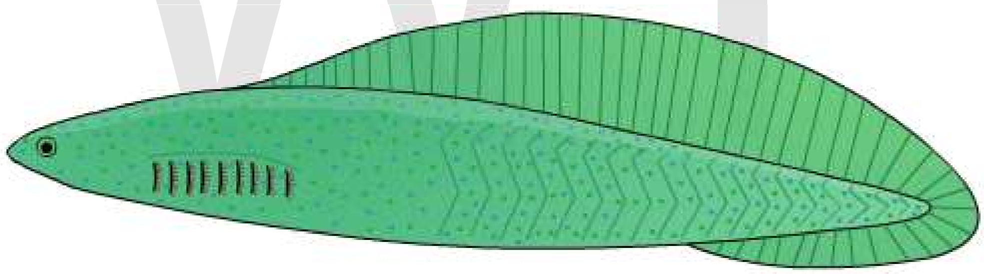
History of paleontology

Although paleontology became established around 1800, earlier thinkers had noticed aspects of the fossil record. The ancient Greek philosopher Xenophanes (570–480 BC) concluded from fossil sea shells that some areas of land were once under water. During the Middle Ages the Persian naturalist Ibn Sina, known as *Avicenna* in Europe, discussed fossils and proposed a theory of petrifying fluids on which Albert of Saxony elaborated in the 14th century. The Chinese naturalist Shen Kuo (1031–1095) proposed a theory of climate change based on the presence of petrified bamboo in regions that in his time were too dry for bamboo.

In early modern Europe, the systematic study of fossils emerged as an integral part of the changes in natural philosophy that occurred during the Age of Reason. At the end of the 18th century Georges Cuvier's work established comparative anatomy as a scientific discipline and, by proving that some fossil animals resembled no living ones, demonstrated that animals could become extinct, leading to the emergence of paleontology. The expanding knowledge of the fossil record also played an increasing role in the development of geology, particularly stratigraphy.

The first half of the 19th century saw geological and paleontological activity become increasingly well organized with the growth of geologic societies and museums and an increasing number of professional geologists and fossil specialists. Interest increased for reasons that were not purely scientific, as geology and paleontology helped industrialists to find and exploit natural resources such as coal.

This contributed to a rapid increase in knowledge about the history of life on Earth and to progress in the definition of the geologic time scale, largely based on fossil evidence. In 1822 Henri Marie Ducrotay de Blanville, editor of *Journal de Phisique*, coined the word "paleontology" to refer to the study of ancient living organisms through fossils. As knowledge of life's history continued to improve, it became increasingly obvious that there had been some kind of successive order to the development of life. This encouraged early evolutionary theories on the transmutation of species. After Charles Darwin published *Origin of Species* in 1859, much of the focus of paleontology shifted to understanding evolutionary paths, including human evolution and evolutionary theory.



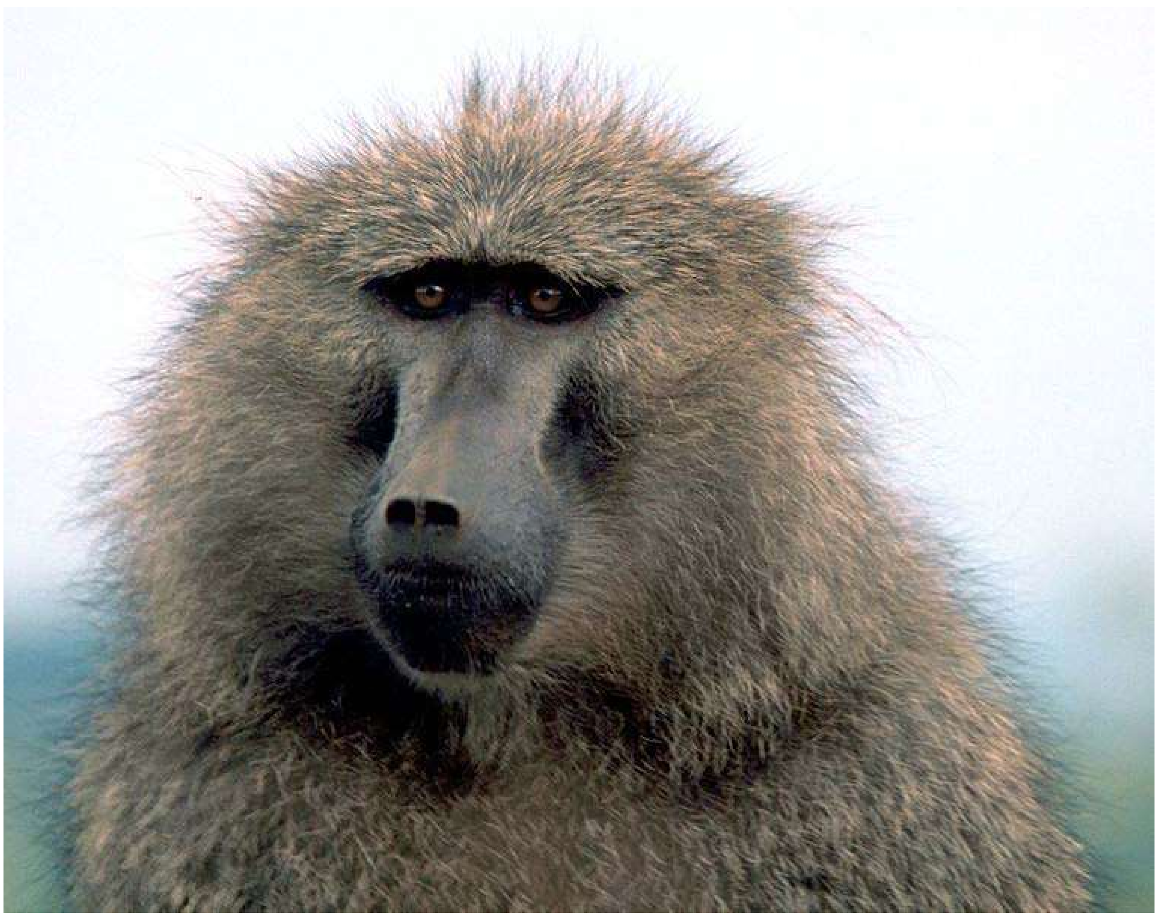
Haikouichthys, from about 518 million years ago in China, may be the earliest known fish.

The last half of the 19th century saw a tremendous expansion in paleontological activity, especially in North America. The trend continued in the 20th century with additional regions of the Earth being opened to systematic fossil collection. Fossils found in China near the end of the 20th century have been particularly important as they have provided new information about the earliest evolution of animals, early fish, dinosaurs and the evolution of birds. The last few decades of the 20th century saw a renewed interest in mass extinctions and their role in the evolution of life on Earth. There was also a renewed interest in the Cambrian explosion that apparently saw the development of the body plans of most animal phyla. The discovery of fossils of the Ediacaran biota and developments in paleobiology extended knowledge about the history of life back far before the Cambrian.

Increasing awareness of Gregor Mendel's pioneering work in genetics led first to the development of population genetics and then in the mid-20th century to the modern evolutionary synthesis, which explains evolution as the outcome of events such as mutations and horizontal gene transfer which provide genetic variation, with genetic drift and natural selection driving changes in this variation over time. Within the next few years the role and operation of DNA in genetic inheritance were discovered, leading to what is now known as the "Central Dogma" of molecular biology. In the 1960s molecular phylogenetics, the investigation of evolutionary "family trees" by techniques derived from biochemistry, began to make an impact, particularly when it was proposed that the human lineage had diverged from apes much more recently than was generally thought at the time. Although this early study compared proteins from apes and humans, most molecular phylogenetics research is now based on comparisons of RNA and DNA.

Chapter- 3

Primatology



Primatology is the branch of zoology and Anthropology concerned with the study of primates. It is a diverse discipline and **primatologists** can be found in departments of biology, anthropology, psychology and many others. The fields cross over in the study of the hominids, which include all ape-like ancestors of man and the other great apes.

Modern primatology is an extremely diverse science. It ranges from anatomical studies of primate ancestors and field studies of primates in their natural habitat, to experiments in animal psychology and ape language. It has cast an immense amount of light on basic human behaviors and ancient ancestry of these behaviors.

Disciplines

Primatology as a science has many different disciplines that stem from the differing cultural backgrounds of the founders of the field. Indeed, the study itself seems to change throughout different areas of the world, as different approaches, theories and methods are used in the researching of non-human primates and their relationships and links with humans.

There are two main disciplines within the field of primatology, Western primatology and Japanese primatology. These two divergent disciplines stem from their unique cultural backgrounds and philosophies that went into their founding. Although, fundamentally, both Western and Japanese primatology share many of the same principles, the areas of their focus in primate research and their methods of obtaining data differ widely.

Western primatology

Origins

Western primatology stems primarily from colonial research into primate behavior, especially by American colonial scientists. Early primate study focused primarily in medical research, but some scientists also conducted "civilizing" experiments on chimpanzees in order to gauge both primate intelligence and the limits of their brainpower.

Theory

The study of primatology looks at the biological and psychological aspects of non-human primates. The focus is on studying the common links between humans and primates. It is believed that by understanding our closest animal relatives, we might better understand the nature shared with our ancestors. There have been some cultural and religious issues within the field of primatology, especially as it pertains to evolution.

Methods

Western primatology is an objective science. The general belief is that the scientific observation of nature must be either extremely limited, or completely controlled. Either way, the observers must be neutral to their subjects. This allows for data to be unbiased and for the subjects to be uninfluenced by human interference.

There are three methodological approaches in primatology: field study, the more realistic approach, laboratory study, the more controlled approach and semi-free ranging, where primate habitat and wild social structure is replicated in a captive setting.

Field is done in natural environments, in which scientific observers watch primates in their natural habitat.

Laboratory study is done in controlled lab settings. In lab settings, scientists are able to perform controlled experimentation on the learning capabilities and behavioral patterns of the animals.

In semi-free ranging studies, scientists are able to watch how primates would act in the wild but have continual access to them, the ability to do lifetime studies and the ability to control their environments. Such facilities include the Living Links Center at the Yerkes National Primate Research Center in Georgia and the Elgin Center at Lion Country Safari in Florida.

All types of primate study in the Western methodology are meant to be very neutral. Although there are certain Western primatologists who do more subjective research, the emphasis in this discipline is on the objective.

Early primatology tended to focus on individual researchers and their exploits. Stories of researchers such as Dian Fossey and Jane Goodall are examples of this. Long-term sites of research tend to be best associated with their founders and this leads to some tension between younger primatologists and the veterans in the field.

Notable Western primatologists

- Jeanne Altmann
- Jean Baulu
- Irwin Bernstein
- Michelle Bezanson
- Sarah Blaffer Hrdy
- Christophe Boesch
- Gottfried Hohmann
- Geoffrey Bourne
- C. R. Carpenter
- Colin Chapman
- Dorothy Cheney
- Marina Cords
- Thomas Defler
- Frans de Waal
- Linda Fedigan
- Dian Fossey
- Boris Lapin
- Agustin Fuentes
- Birutė Galdikas
- Paul Garber
- Thomas R. Gillespie
- Jane Goodall
- Colin Groves
- Alejandro Estrada
- Alexander Harcourt

- Philip Hershkovitz
- Lynne Isbell
- Hans Kummer
- Nadezhda Ladygina-Kohts
- Bill McGrew
- John Mitani
- Russell Mittermeier
- Matthew Richardson
- Anne E. Russon
- Anthony Rylands
- Robert Sapolsky
- Carel van Schaik
- Robert Seyfarth
- Meredith Small
- Barbara Smuts
- Craig Stanford
- Karen Strier
- Tom Struhsaker
- Michael Tomasello
- Omar Wasow
- Sherwood Washburn
- David P. Watts
- Barbara J. Welker
- Richard Wrangham
- Gabriel Zunino

Japanese primatology

Origins

The discipline of Japanese primatology was developed out of animal ecology. It is mainly credited to Kinji Imanishi and Junichiro Itani. Imanishi was an animal ecologist who began studying wild horses before focusing more on primate ecology. He helped found the Primate Research Group in 1950. Junichiro was a renowned anthropologist and a professor at Kyoto University. He is a co-founder of the Primate Research Institute and the Centre for African Area Studies.

Theory

The Japanese discipline of primatology tends to be more interested in the social aspects of primates. Social evolution and anthropology are of primary interest to them. The Japanese theory believes that studying primates will give us insight into the duality of human nature: individual self vs. social self.

The traditional and cultural aspects of Japanese science lend themselves to an "older sibling" mentality. It is believed that animals should be treated with respect, but also a firm authority. This is not to say that the Japanese study of primatology is cruel – far from it – just that it doesn't feel that their subjects should be given reverential treatment.

One particular Japanese primatologist, Kawai Masao, introduced the concept of *kyokan*. This was the theory that the only way to attain reliable scientific knowledge was to attain a mutual relation, personal attachment and shared life with the animal subjects. Though Kawai is the only Japanese primatologist associated with the use of this term, the underlying principle is part of the foundation of Japanese primate research.

Methods

Japanese primatology is a carefully disciplined subjective science. It is believed that the best data comes through identification with your subject. Neutrality is eschewed in favour of a more casual atmosphere, where researcher and subject can mingle more freely. Domestication of nature is not only desirable, but necessary for study.

Japanese primatologists are renowned for their ability to recognise animals by sight and indeed most primates in a research group are usually named and numbered. Comprehensive data on every single subject in a group is uniquely Japanese trait of primate research. Each member of the primate community has a part to play and the Japanese researchers are interested in this complex interaction.

For Japanese researchers in primatology, the findings of the team are emphasised over the individual. The study of primates is a group effort and the group will get the credit for it. It is also not unusual to see a team of researchers observing the same group of primates for several years in order to get very detailed demographic and social histories.

Notable Japanese primatologists

- Imanishi, Kinji
- Junichiro, Itani
- Masao, Kawai
- Tetsuro Matsuzawa
- Toshisada Nishida
- Hiraiwa-Hasegawa, Mariko
- Jensen, Erik

Primatology in sociobiology

Where sociobiology attempts to understand the actions of all animal species within the context of advantageous and disadvantageous behaviors, primatology takes an exclusive look at the order Primates, which includes *Homo sapiens*. The interface between primatology and sociobiology examines in detail the evolution of primate behavioral processes and what studying our closest living primate relatives can tell about our own minds. As the American anthropologist Earnest Albert Hooton used to say: "Primas sum: primatum nil a me alienum puto" ("I am a primate; nothing about primates is outside of my bailiwick"). The meeting point of these two disciplines has become a nexus of discussion on key issues concerning the evolution of sociality, the development and purpose of language and deceit and the development and propagation of culture.

Additionally, this interface is of particular interest to the science watchers in science and technology studies, who examine the social conditions which incite, mould and eventually react to scientific discoveries and knowledge. The STS approach to primatology and sociobiology stretches beyond studying the apes, into the realm of observing the people studying the apes.

Taxonomic basis

Before Darwin and before molecular biology, the father of modern taxonomy, Carolus Linnaeus, organized natural objects into kinds, that we now know reflect their evolutionary relatedness. He sorted these kinds by morphology, the shape of the object. Animals such as monkeys, chimpanzees and orangutans resemble humans closely, so Linnaeus placed *Homo sapiens* together with other similar-looking organisms into the taxonomic order *Primates*. Modern molecular biology reinforced humanity's place within the Primate order. Humans and simians share the vast majority of their DNA, with chimpanzees sharing between 97-99% genetic identity with humans.

From grooming to speaking

Although social grooming is observed in many animal species, the grooming activities undertaken by primates are not strictly for the elimination of parasites. In primates, grooming is a social activity that strengthens relationships. The amount of grooming taking place between members of a troop is a potent indicator of alliance formation or troop solidarity. Robin Dunbar suggests a link between primate grooming and the development of human language. The size of the neocortex in a primate's brain correlates directly to the number of individuals it can keep track of socially, be it a troop of chimps or a tribe of humans.

This number is referred to as the monkeysphere. If a population exceeds the size outlined by its cognitive limitations, the group undergoes a schism. Set into an evolutionary context, the Dunbar number shows a drive for the development of a method of bonding that is less labor intensive than grooming: language. As the monkeysphere grows, the amount of time that would need to be spent grooming troopmates soon becomes unmanageable. Furthermore, it is only possible to bond with one troopmate at a time while grooming. The evolution of vocal communication solves both the time constraint and the one-on-one problem, but at a price.

Language allows for bonding with multiple people at the same time at a distance, but the bonding produced by language is less intense. This view of language evolution covers the general biological trends needed for language development, but it takes another hypothesis to uncover the evolution of the cognitive processes necessary for language.

Modularity of the primate mind

Noam Chomsky's concept of innate language addresses the existence of universal grammar, which suggests a special kind of "device" all humans are born with whose sole purpose is language. Fodor's modular mind hypothesis expands on this concept, suggesting the existence of preprogrammed modules for dealing with many, or all aspects of cognition. Although these modules do not need to be physically distinct, they must be functionally distinct. Orangutans are currently being taught language at the Smithsonian National Zoo using a computer system developed by primatologist Dr. Francine Neago in conjunction with IBM.

The massive modularity theory thesis posits that there is a huge number of tremendously interlinked but specialized modules running programs called Darwinian algorithms, or DA. DA can be selected for just as a gene can, eventually improving cognition. The contrary theory, of generalist mind, suggests that the brain is just a big computer that runs one program, the mind. If the mind is a general computer, for instance, the ability to use reasoning should be identical regardless of the context. This is not what is observed. When faced with abstract numbers and letters with no "real world" significance, respondents of the Wason card test generally do very poorly. However, when exposed to a test with an identical rule set but socially relevant content, respondents score markedly higher. The difference is especially pronounced when the content is about reward and payment. This test strongly suggests that human logic is based on a module originally developed in a social environment to root out cheaters and that either the module is at a huge disadvantage where abstract thinking is involved, or that other less effective modules are used when faced with abstract logic.

Further evidence supporting the modular mind has steadily emerged with some startling revelations concerning primates. A very recent study indicated that human babies and grown monkeys approach and process numbers in a similar fashion, suggesting an evolved set of DA for mathematics (Jordan). The conceptualization of both human infants and primate adults is cross-sensory, meaning that they can add 15 red dots to 20 beeps and approximate the answer to be 35 grey squares. As more evidence of basic cognitive modules are uncovered, they will undoubtedly form a more solid foundation upon which the more complex behaviors can be understood.

In contradiction to this, neuroscientist Jaak Panksepp has argued that the mind is not a computer nor is it massively modular. He states that no evidence of massive modularity or the brain as a digital computer has been gained through actual neuroscience, as opposed to psychological studies. He criticises psychologists who use the massive modularity thesis for not integrating neuroscience into their understanding.

The primate theory of mind

Primate behavior, like human behavior, is highly social and ripe with the intrigue of kingmaking, powerplays, deception, cuckoldry and apology. In order to understand the staggeringly complex nature of primate interactions, we look to theory of mind. Theory of mind asks whether or not an individual recognizes and can keep track of information asymmetry amongst individuals in the group and whether or not they can attribute folk psychological states to their peers. If some primates can tell what others know and want and act accordingly, they can gain advantage and status.

Recently, chimpanzee theory of mind has been advanced by Felix Warneken of the Max Planck Institute. His studies have shown that chimpanzees can recognize whether a researcher desires a dropped object and act accordingly by picking it up. Even more compelling is the observation that chimps will only act if the object is dropped in an accidental-looking manner: if the researcher drops the object in a way that appears intentional, the chimp will ignore the object.

In a related experiment, groups of chimps were given rope-pulling problems they could not solve individually. Warneken's subjects rapidly figured out which individual in the group was the best rope puller and assigned it the bulk of the task. This research is highly indicative of the ability of chimps to detect the folk psychological state of "desire", as well as the ability to recognize that other individuals are better at certain tasks than they are.

However primates do not always fare so well in situations requiring theory of mind. In one experiment pairs of chimpanzees who had been close grooming partners were offered two levers. Pressing one lever would bring them food and another would bring their grooming partner food. Pressing the lever to clearly give their grooming partner much-wanted food would not take away from how much food they themselves got. For some reason, the chimps were unwilling to depress the lever that would give their long-time chums food. It is plausible but unlikely that the chimps figured there was finite food and it would eventually decrease their own food reward. The experiments are open to such interpretations making it hard to establish anything for certain.

One phenomenon which would indicate a possible fragility of theory of mind in primates occurs when a baboon gets lost. Under such circumstances, the lost baboon generally makes "call barks" to announce that it is lost. Previous to the 1990s it was thought that these call barks would then be returned by the other baboons, similar to the case is in vervet monkeys. However when researchers studied this formally in the past few years they found something surprising: Only the baboons who were lost would ever give call barks. Even if an infant was wailing in agony just a few hundred meters away, its mother who would clearly recognise its voice and would be frantic about his safety (or alternatively run towards her infant depending on her own perceived safety), would often simply stare in his direction visibly agitated. If the anguishing baboon mother made any type of call at all, the infant would instantly recognise her and run to her position. This type of logic appears to be lost on the baboon, suggesting a serious gap in theory of mind of this otherwise seemingly very intelligent primate species. However, it is also possible that baboons do not return call barks for ecological reasons, for example because returning the call bark might call attention to the lost baboon, putting it at greater risk from predators.

Criticisms

Scientific studies concerning primate and human behavior have been subject to the same set of political and social complications, or biases, as every other scientific discipline. The borderline and multidisciplinary nature of primatology and sociobiology make them ripe fields of study because they are amalgams of objective and subjective sciences. Current scientific practice, especially in the hard sciences, requires a total dissociation of personal experience from the finished scientific product (Bauchspies 8). This is a strategy that is incompatible with observational field studies and weakens them in the eyes of hard science. As mentioned above, the Western school of primatology tries to minimize or control subjectivity to the greatest degree possible, while the Japanese school of primatology tends to embrace the closeness inherent in studying nature.

Social critics of science, some operating from within the field, cry foul when reviewing the young disciplines of primatology and sociobiology. Claims are made that researchers form opinions on issues concerning human sociality prior to doing their studies and then seek evidence that agrees with their worldview or otherwise furthers a sociopolitical agenda. In particular, the use of primatological studies to assert gender roles and promote or subvert feminism has been a serious point of contention.

An example of this is Zuckerman’s 1932 study of captive hamadryas baboons, as critiqued in Sturm and Fedigan's Changing Views on Primate Societies. Zuckerman observed male baboons kill each other off in great number in their captive environment. Whether intended or not, the study served to reinforce images of the male as the sole competitor in an often violent race to secure dominance and access to a harem of females. Despite wildly unrealistic overcrowding and completely incorrect male to female ratio, Zuckerman's paper was viewed as good science at the time. These ideas were used to justifiy the status quo of human male dominance and consequently, the studies were widely supported and assumed to be the basis of a primate-wide template for behavior, including that of humans. Incidentally, the hamadryas baboon females are among the most submissive and most gender-unequal of all primates, although primates and humans share a tremendous variation in troop structure (Hrdy 101, Stone).

A significant 2002 paper comparing primate/human cognition was retracted in August, 2010. Its lead author, Harvard University psychologist Marc Hauser, "is taking a year-long leave after a lengthy internal investigation found evidence of scientific misconduct in his laboratory." Videotaped control data supporting the authors' conclusion that cotton-top tamarin monkeys displayed pattern-learning behavior similar to human infants reportedly was unable to be located after a three-year investigation.

Chapter- 4

Sociocultural Evolution

Sociocultural evolution(ism) is an umbrella term for theories of **cultural evolution** and social evolution, describing how cultures and societies have changed over time. Note that "sociocultural evolution" is not an equivalent of "sociocultural development" (unified processes of differentiation and integration involving increases in sociocultural complexity), as sociocultural evolution also encompasses sociocultural transformations accompanied by decreases of complexity (degeneration) as well as ones not accompanied by any significant changes of sociocultural complexity (cladogenesis). Thus, **sociocultural evolution** can be defined as "the process by which structural reorganization is affected through time, eventually producing a form or structure which is qualitatively different from the ancestral form.... Evolutionism then becomes the scientific activity of finding nomothetic explanations for the occurrence of such structural changes". Although such theories typically provide models for understanding the relationship between technologies, social structure, the values of a society and how and why they change with time, they vary as to the extent to which they describe specific mechanisms of variation and social change.

Sociocultural modeling is an umbrella term for theories of cultural and social evolution, which aims to describe how cultures and societies have developed over time. Such theories typically provide models for understanding the relationship between technologies, social structure, the beliefs, values and goals of a society and how and why they change with time. Such models are of particular interest to the military in helping unstable regions transition to more stable sustainable states. Most 19th century and some 20th century approaches aimed to provide models for the evolution of humankind as a whole, arguing that different societies are at different stages of social development. At present this thread is continued to some extent within the World System approach. Many of the more recent 20th-century approaches focus on changes specific to individual societies and reject the idea of directional change, or social progress. Most archaeologists and cultural anthropologists work within the framework of modern theories of sociocultural evolution. Modern approaches to sociocultural evolution include neoevolutionism, sociobiology, theory of modernization and theory of postindustrial society.

Introduction

Anthropologists and sociologists often assume that human beings have natural social tendencies and that particular human social behaviours have non-genetic causes and dynamics (i.e. they are learned in a social environment and through social interaction). Societies exist in complex social environments (i.e. with natural resources and constraints) and adapt themselves to these environments. It is thus inevitable that all societies change.

Specific theories of social or cultural evolution are usually meant to explain differences between coeval societies, by positing that different societies are at different stages of development. Although such theories typically provide models for understanding the relationship between technologies, social structure, or values of a society, they vary as to the extent to which they describe specific mechanisms of variation and change.

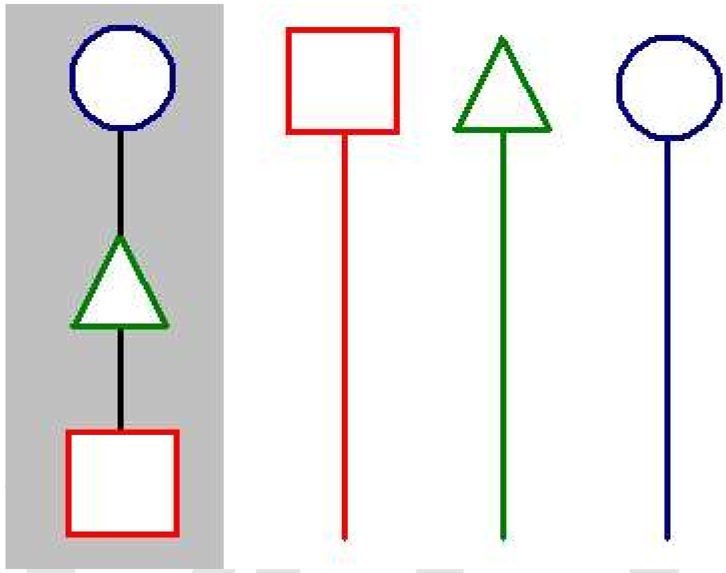
Early sociocultural evolution theories—the theories of Auguste Comte, Herbert Spencer and Lewis Henry Morgan—developed simultaneously but independently of Charles Darwin's works and were popular from the late 19th century to the end of World War I. These 19th-century unilineal evolution theories claimed that societies start out in a *primitive* state and gradually become more *civilized* over time and equated the culture and technology of Western civilization with progress. Some forms of early sociocultural evolution theories (mainly unilineal ones) have led to much criticised theories like social Darwinism and scientific racism, used in the past to justify existing policies of colonialism and slavery and to justify new policies such as eugenics.

Most 19th-century and some 20th-century approaches aimed to provide models for the evolution of humankind as a single entity. However, most 20th-century approaches, such as multilineal evolution, focused on changes specific to individual societies. Moreover, they rejected directional change (i.e. orthogenetic, teleological or progressive change). Most archaeologists work within the framework of multilineal evolution. Other contemporary approaches to social change include neoevolutionism, sociobiology, dual inheritance theory, theory of modernisation and theory of postindustrial society.

Richard Dawkins wrote in *The Selfish Gene* in 1976 that "there are some examples of cultural evolution in birds and monkeys, but ... it is our own species that really shows what cultural evolution can do".

Classical social evolutionism

Development



In the unilineal evolution model at left, all cultures progress through set stages, while in the multilineal evolution model at right, distinctive culture histories are emphasized.

Organic society

The 14th century Islamic scholar Ibn Khaldun concluded that societies are living organisms that experience cyclic birth, growth, maturity, decline and ultimately death due to universal causes several centuries before the Western civilisation developed the science of sociology. Nonetheless, theories of social and cultural evolution were common in modern European thought. Prior to the 18th century, Europeans predominantly believed that societies on Earth were in a state of decline. European society held up the world of antiquity as a standard to aspire to and Ancient Greece and Ancient Rome produced levels of technical accomplishment which Europeans of the Middle Ages sought to emulate. At the same time, Christianity taught that people lived in a debased world fundamentally inferior to the Garden of Eden and Heaven. During The Age of Enlightenment, however, European self-confidence grew and the notion of progress became increasingly popular. It was during this period that what would later become known as "sociological and cultural evolution" would have its roots.

Stadial theory

The Enlightenment thinkers often speculated that societies progressed through stages of increasing development and looked for the logic, order and the set of scientific truths that determined the course of human history. Georg Wilhelm Friedrich Hegel, for example, argued that social development was an inevitable and determined process, similar to an acorn which has no choice but to become an oak tree. Likewise, it was assumed that societies start out primitive, perhaps in a Hobbesian state of nature and naturally progress toward something resembling industrial Europe.

While earlier authors such as Michel de Montaigne discussed how societies change through time, it was truly the Scottish Enlightenment which proved key in the development of sociocultural evolution. After Scotland's union with England in 1707, several Scottish thinkers pondered what the relationship between progress and the 'decadence' brought about by increased trade with England and the affluence it produced. The result was a series of "conjectural histories". Authors such as Adam Ferguson, John Millar and Adam Smith argued that all societies pass through a series of four stages: hunting and gathering, pastoralism and nomadism, agricultural and finally a stage of commerce. These thinkers thus understood the changes Scotland was undergoing as a transition from an agricultural to a mercantile society.

Auguste Comte

Philosophical concepts of progress (such as those expounded by the German philosopher G.W.F. Hegel) developed as well during this period. In France authors such as Claude Adrien Helvétius and other philosophes were influenced by this Scottish tradition. Later thinkers such as Comte de Saint-Simon developed these ideas. Auguste Comte in particular presented a coherent view of social progress and a new discipline to study it—sociology.

These developments took place in a wider context. The first process was colonialism. Although imperial powers settled most differences of opinion with their colonial subjects with force, increased awareness of non-Western peoples raised new questions for European scholars about the nature of society and culture. Similarly, effective administration required some degree of understanding of other cultures. Emerging theories of sociocultural evolution allowed Europeans to organise their new knowledge in a way that reflected and justified their increasing political and economic domination of others: colonised people were less evolved, colonising people were more evolved. When the 17th-century English philosopher Thomas Hobbes described indigenous people as having "no arts, no letters, no society" and their life as "solitary, poor, nasty, brutish and short", he was defining the stereotype of a "savage," one that would last for many years. Modern civilization, understood as the Western civilization, was the result of steady progress from such a state and such a notion was common to many thinkers of the Enlightenment, including Voltaire.

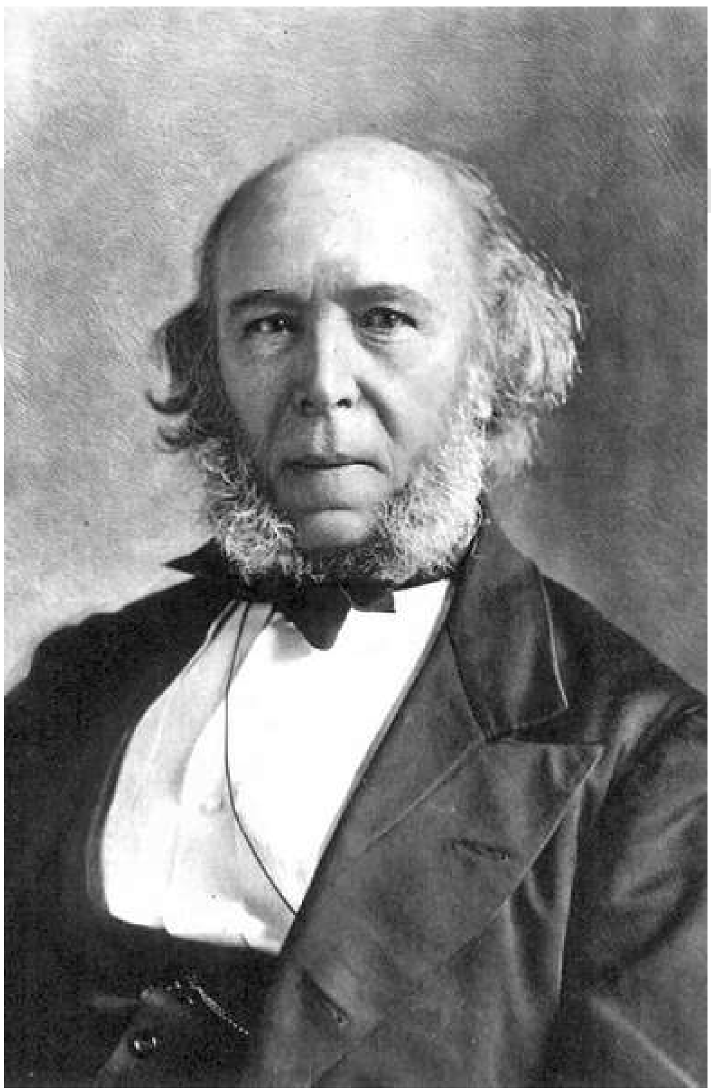
The second process was the Industrial Revolution and the rise of capitalism which allowed and promoted continual revolutions in the means of production. Emerging theories of sociocultural evolution reflected a belief that the changes in Europe wrought by the Industrial Revolution and capitalism were improvements. Industrialisation, combined with the intense political change brought about by the French Revolution and the U.S. Constitution, which were paving the way for the dominance of democracy, forced European thinkers to reconsider some of their assumptions about how society was organised.

Eventually, in the 19th century three great classical theories of social and historical change were created: sociocultural evolutionism, the social cycle theory and Marxist historical materialism. Those theories had one common factor: they all agreed that the history of humanity is pursuing a certain fixed path, most likely that of social progress. Thus, each past event is not only chronologically, but causally tied to the present and future events. Those theories postulated that by recreating the sequence of those events, sociology could discover the laws of history.

Sociocultural evolutionism and the idea of progress

While sociocultural evolutionists agree that an evolution-like process leads to social progress, classical social evolutionists have developed many different theories, known as theories of unilineal evolution. Sociocultural evolutionism was the prevailing theory of early sociocultural anthropology and social commentary and is associated with scholars like Auguste Comte, Edward Burnett Tylor, Lewis Henry Morgan, Benjamin Kidd, L.T.

Hobhouse and Herbert Spencer. Sociocultural evolutionism attempted to formalise social thinking along scientific lines, with the added influence from the biological theory of evolution. If organisms could develop over time according to discernible, deterministic laws, then it seemed reasonable that societies could as well. Human society was compared to a biological organism and social science equivalents of concepts like variation, natural selection and inheritance were introduced as factors resulting in the progress of societies. Idea of progress led to that of a fixed "stages" through which human societies progress, usually numbering three—savagery, barbarism and civilization—but sometimes many more. As early as the late 18th century Marquis de Condorcet listed 10 stages, or "epochs", each advancing the rights of man and perfecting the human race. At that time, anthropology was rising as a new scientific discipline, separating from the traditional views of "primitive" cultures that was usually based on religious views.



Herbert Spencer

Classical social evolutionism is most closely associated with the 19th-century writings of Auguste Comte, Herbert Spencer (coiner of the phrase "survival of the fittest"). In many ways Spencer's theory of "cosmic evolution" has much more in common with the works of Jean-Baptiste Lamarck and Auguste Comte than with contemporary works of Charles Darwin. Spencer also developed and published his theories several years earlier than Darwin. In regard to social institutions, however, there is a good case that Spencer's writings might be classified as 'Social Evolutionism'. Although he wrote that societies over time progressed and that progress was accomplished through competition, he stressed that the individual (rather than the collectivity) is the unit of analysis that evolves, that evolution takes place through natural selection and that it affects social as well as biological phenomenon. Nonetheless, the publication of Darwin's works proved a boon to the proponents of sociocultural evolution. The ideas of biological evolution was seen as an attractive explanation for many questions about the development of society

Both Spencer and Comte view the society as a kind of organism subject to the process of growth—from simplicity to complexity, from chaos to order, from generalisation to specialisation, from flexibility to organisation. They agreed that the process of societies growth can be divided into certain stages, have their beginning and eventual end and that this growth is in fact social progress—each newer, more evolved society is better. Thus progressivism became one of the basic ideas underlying the theory of sociocultural evolutionism.

Auguste Comte, known as father of sociology, formulated the law of three stages: human development progresses from the theological stage, in which nature was mythically conceived and man sought the explanation of natural phenomena from supernatural beings, through metaphysical stage in which nature was conceived of as a result of obscure forces and man sought the explanation of natural phenomena from them until the final positive stage in which all abstract and obscure forces are discarded and natural phenomena are explained by their constant relationship. This progress is forced through the development of human mind and increasing application of thought, reasoning and logic to the understanding of the world. For Comte, it was the science-valuing society that was the highest, most developed type of human organization.

Herbert Spencer, who argued against government intervention, believing that society evolution should be toward increasing individual freedom, differentiated between two phases of development, focusing on the type of internal regulation within societies. Thus he differentiated between military and industrial societies. The earlier, more primitive military society has a goal of conquest and defence, is centralised, economically self-sufficient, collectivistic, puts the good of a group over the good of an individual, uses compulsion, force and repression, rewards loyalty, obedience and discipline. The industrial society has a goal of production and trade, is decentralised, interconnected with other societies via economic relations, achieves its goals through voluntary cooperation and individual self-restraint, treats the good of individual as the highest value, regulates the social life via voluntary relations, values initiative, independence and innovation. The transition process from the military to industrial society is the outcome of steady evolutionary processes within the society.

Regardless of how scholars of Spencer interpret his relation to Darwin, Spencer proved to be an incredibly popular figure in the 1870s, particularly in the United States. Authors such as Edward L. Youmans, William Graham Sumner, John Fiske, John W. Burgess, Lester Frank Ward, Lewis H. Morgan and other thinkers of the gilded age all developed similar theories of social evolutionism as a result of their exposure to Spencer as well as Darwin.

Lewis H. Morgan

Lewis H. Morgan, an anthropologist whose ideas have had much impact on sociology, in his 1877 classic *Ancient Societies* differentiated between three eras: savagery, barbarism and civilization, which are divided by technological inventions, like fire, bow, pottery in the savage era, domestication of animals, agriculture, metalworking in the barbarian era and alphabet and writing in the civilization era. Thus Morgan introduced a link between social progress and technological progress. Morgan viewed technological progress as a force behind social progress and any social change—in social institutions, organisations or ideologies—has its beginnings in technological change. Morgan's theories were popularised by Friedrich Engels, who based his famous work *The Origin of the Family, Private Property and the State* on it. For Engels and other Marxists, this theory was important as it supported their conviction that materialistic factors—economic and technological—are decisive in shaping the fate of humanity.

Émile Durkheim, another of the "fathers" of sociology, developed a similar, dichotomal view of social progress. His key concept was social solidarity, as he defined social evolution in terms of progressing from mechanical solidarity to organic solidarity. In mechanical solidarity, people are self-sufficient, there is little integration and thus there is the need for use of force and repression to keep society together. In organic solidarity, people are much more integrated and interdependent and specialisation and cooperation is extensive. Progress from mechanical to organic solidarity is based first on population growth and increasing population density, second on increasing "morality density" (development of more complex social interactions) and thirdly, on the increasing specialisation in workplace. To Durkheim, the most important factor in the social progress is the division of labour.

Émile Durkheim

Anthropologists Sir E.B. Tylor in England and Lewis Henry Morgan in the United States worked with data from indigenous people, who they claimed represented earlier stages of cultural evolution that gave insight into the process and progression of evolution of culture. Morgan would later have a significant influence on Karl Marx and Friedrich Engels, who developed a theory of sociocultural evolution in which the internal contradictions in society created a series of escalating stages that ended in a socialist society. Tylor and Morgan elaborated the theory of unilinear evolution, specifying criteria for categorising cultures according to their standing within a fixed system of growth of humanity as a whole and examining the modes and mechanisms of this growth. Theirs was often a concern with culture in general, not with individual cultures.

Their analysis of cross-cultural data was based on three assumptions:

1. contemporary societies may be classified and ranked as more "primitive" or more "civilized";
2. There are a determinate number of stages between "primitive" and "civilized" (e.g. band, tribe, chiefdom and state),
3. All societies progress through these stages in the same sequence, but at different rates.

Theorists usually measured progression (that is, the difference between one stage and the next) in terms of increasing social complexity (including class differentiation and a complex division of labour), or an increase in intellectual, theological and aesthetic sophistication. These 19th-century ethnologists used these principles primarily to explain differences in religious beliefs and kinship terminologies among various societies.

Lester Frank Ward developed Spencer's theory but unlike Spencer, who considered evolution to be general process applicable to the entire world, physical and sociological, Ward differentiated sociological evolution from biological evolution. He stressed that humans create goals for themselves and strive to realise them, whereas there is no such intelligence and awareness guiding the non-human world, which develops more or less at random. He created a hierarchy of evolution processes. First, there is cosmogenesis, creation and evolution of the world. Then, when life arises, there is biogenesis. Development of humanity leads to anthropogenesis, which is influenced by the human mind. Finally, when society develops, so does sociogenesis, which is the science of shaping the society to fit with various political, cultural and ideological goals.

Edward Burnett Tylor

Edward Burnett Tylor, pioneer of anthropology, focused on the evolution of culture worldwide, noting that culture is an important part of every society and that it is also subject to the process of evolution. He believed that societies were at different stages of cultural development and that the purpose of anthropology was to reconstruct the evolution of culture, from primitive beginnings to the modern state.

Ferdinand Tönnies describes evolution as the development from informal society, where people have many liberties and there are few laws and obligations, to modern, formal rational society, dominated by traditions and laws and people are restricted from acting as they wish. He also notes that there is a tendency of standardisation and unification, when all smaller societies are absorbed into a single, large, modern society. Thus Tönnies can be said to describe part of the process known today as globalization. Tönnies was also one of the first sociologists to claim that the evolution of society is not necessarily going in the right direction, that social progress is not perfect and it can even be called a regression as the newer, more evolved societies are obtained only after paying a high cost, resulting in decreasing satisfaction of individuals making up that society. Tönnies' work became the foundation of neoevolutionism.

Although not usually counted as a sociocultural evolutionist, Max Weber's theory of tripartite classification of authority can be viewed as an evolutionary theory as well. Weber distinguishes three ideal types of political leadership, domination and authority: charismatic domination (familial and religious), traditional domination (patriarchs, patrimonalism, feudalism) and legal (rational) domination (modern law and state, bureaucracy). He also notes that legal domination is the most advanced and that societies evolve from having mostly traditional and charismatic authorities to mostly rational and legal ones.

Critique and impact on modern theories

The early 20th century inaugurated a period of systematic critical examination and rejection of the sweeping generalisations of the unilineal theories of sociocultural evolution. Cultural anthropologists such as Franz Boas, along with his students, including Ruth Benedict and Margaret Mead, are regarded as the leaders of anthropology's rejection of classical social evolutionism.

They used sophisticated ethnography and more rigorous empirical methods to argue that Spencer, Tylor and Morgan's theories were speculative and systematically misrepresented ethnographic data. Theories regarding "stages" of evolution were especially criticised as illusions. Additionally, they rejected the distinction between "primitive" and "civilized" (or "modern"), pointing out that so-called primitive contemporary societies have just as much history and were just as evolved, as so-called civilized societies. They therefore argued that any attempt to use this theory to reconstruct the histories of non-literate (i.e. leaving no historical documents) peoples is entirely speculative and unscientific.

They observed that the postulated progression, which typically ended with a stage of civilization identical to that of modern Europe, is ethnocentric. They also pointed out that the theory assumes that societies are clearly bounded and distinct, when in fact cultural traits and forms often cross social boundaries and diffuse among many different societies (and is thus an important mechanism of change). Boas in his culture history approach focused on anthropological fieldwork in an attempt to identify factual processes instead of what he criticized as speculative stages of growth. His approach was a major influence on the American anthropology in the first half of the 20th century and marked a retreat from high-level generalization and "systems building".

Later critics observed that this assumption of firmly bounded societies was proposed precisely at the time when European powers were colonising non-Western societies and was thus self-serving. Many anthropologists and social theorists now consider unilineal cultural and social evolution a Western myth seldom based on solid empirical grounds. Critical theorists argue that notions of social evolution are simply justifications for power by the elites of society. Finally, the devastating World Wars that occurred between 1914 and 1945 crippled Europe's self-confidence. After millions of deaths, genocide and the destruction of Europe's industrial infrastructure, the idea of progress seemed dubious at best.

Thus modern sociocultural evolutionism rejects most of classical social evolutionism due to various theoretical problems:

1. The theory was deeply ethnocentric—it makes heavy value judgments on different societies; with Western civilization seen as the most valuable.
2. It assumed all cultures follow the same path or progression and have the same goals.
3. It equated civilization with material culture (technology, cities, etc.)
4. It equated evolution with progress or *fitness,* based on deep misunderstandings of evolutionary theory.

Because social evolution was posited as a scientific theory, it was often used to support unjust and often racist social practices—particularly colonialism, slavery and the unequal economic conditions present within industrialized Europe. Social Darwinism is especially criticised, as it led to some philosophies used by the Nazis.

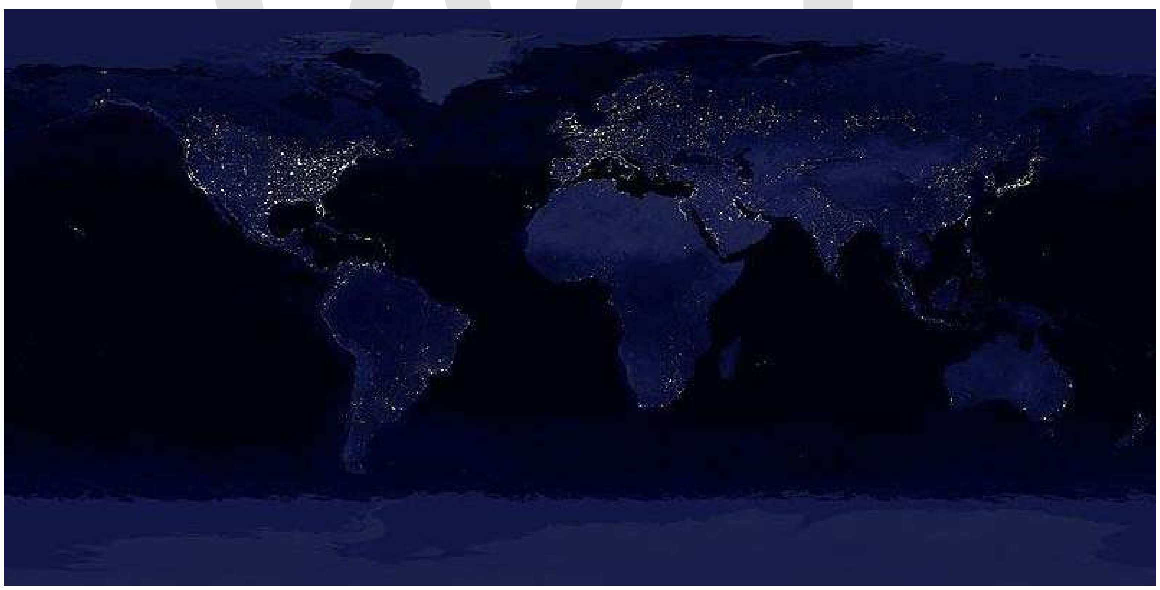
Max Weber, disenchantment and critical theory

Max Weber in 1917

Weber's major works in economic sociology and the sociology of religion dealt with the rationalization, secularisation and so called "disenchantment" which he associated with the rise of capitalism and modernity. In sociology, rationalization is the process whereby an increasing number of social actions become based on considerations of teleological efficiency or calculation rather than on motivations derived from morality, emotion, custom, or tradition. Rather than referring to what is genuinely "rational" or "logical", rationalization refers to a relentless quest for goals that might actually function to the *detriment* of a society. Rationalization is an ambivalent aspect of modernity, manifested especially in Western society; as a behaviour of the capitalist market; of rational administration in the state and bureaucracy; of the extension of modern science; and of the expansion of modern technology.

Weber's thought regarding the rationalizing and secularizing tendencies of modern Western society (sometimes described as the "Weber Thesis") would blend with Marxism to facilitate critical theory, particularly in the work of thinkers such as Jürgen Habermas. Critical theorists, as antipositivists, are critical of the idea of a hierarchy of sciences or societies, particularly with respect to the sociological positivism originally set forth by Comte. Jürgen Habermas has critiqued the concept of pure instrumental rationality as meaning that scientific-thinking becomes something akin to ideology itself. For theorists such as Zygmunt Bauman, rationalization as a manifestation of modernity may be most closely and regrettably associated with the events of the Holocaust.

Modern theories



Composite image of the Earth at night, created by NASA and NOAA. The brightest areas of the Earth are the most urbanized, but not necessarily the most populated. Even more than 100 years after the invention of the electric light, most regions remain thinly populated or unlit.

When the critique of classical social evolutionism became widely accepted, modern anthropological and sociological approaches changed respectively. Modern theories are careful to avoid unsourced, ethnocentric speculation, comparisons, or value judgments;

more or less regarding individual societies as existing within their own historical contexts. These conditions provided the context for new theories such as cultural relativism and multilineal evolution.

In the 1920s and 30s, Gordon Childe revolutionized the study of cultural evolutionism. He conducted a comprehensive pre-history account that provided scholars with evidence for African and Asian cultural transmission into Europe. He combated scientific racism by finding the tools and artifacts of the indigenous people from Africa and Asia and showed how they influenced the technology of European culture. Evidence from his excavations countered the idea of Aryan supremacy and superiority. Childe explained cultural evolution by his theory of divergence with modifications of convergence. He postulated that different cultures form separate methods that meet different needs, but when two cultures were in contact they developed similar adaptations, solving similar problems. Rejecting Spencer's theory of parallel cultural evolution, Childe found that interactions between cultures contributed to the convergence of similar aspects most often attributed to one culture. Childe placed emphasis on human culture as a social construct rather than products of environmental or technological contexts. Childe coined the terms "Neolithic Revolution" and "Urban Revolution" which are still used today in the branch of pre-historic anthropology.

In 1941 anthropologist Robert Redfield wrote about a shift from 'folk society' to 'urban society'. By the 1940s cultural anthropologists such as Leslie White and Julian Steward sought to revive an evolutionary model on a more scientific basis and succeeded in establishing an approach known as neoevolutionism. White rejected the opposition between "primitive" and "modern" societies but did argue that societies could be distinguished based on the amount of energy they harnessed and that increased energy allowed for greater social differentiation (White's law). Steward on the other hand rejected the 19th-century notion of progress and instead called attention to the Darwinian notion of "adaptation", arguing that all societies had to adapt to their environment in some way.

The anthropologists Marshall Sahlins and Elman Service prepared an edited volume, *Evolution and Culture*, in which they attempted to synthesise White's and Steward's approaches. Other anthropologists, building on or responding to work by White and Steward, developed theories of cultural ecology and ecological anthropology. The most prominent examples are Peter Vayda and Roy Rappaport. By the late 1950s, students of Steward such as Eric Wolf and Sidney Mintz turned away from cultural ecology to Marxism, World Systems Theory, Dependency theory and Marvin Harris's Cultural materialism.

Today most anthropologists reject 19th-century notions of progress and the three assumptions of unilineal evolution. Following Steward, they take seriously the relationship between a culture and its environment to explain different aspects of a culture. But most modern cultural anthropologists have adopted a general systems approach, examining cultures as emergent systems and argue that one must consider the whole social environment, which includes political and economic relations among cultures. There are still others who continue to reject the entirety of the evolutionary thinking and look instead at historical contingencies, contacts with other cultures and the operation of cultural symbol systems. As a result, the simplistic notion of "cultural evolution" has grown less useful and given way to an entire series of more nuanced approaches to the relationship of culture and environment. In the area of development studies, authors such as Amartya Sen have developed an understanding of "development" and 'human flourishing' that also question more simplistic notions of progress, while retaining much of their original inspiration.

Neoevolutionism

Neoevolutionism was the first in a series of modern multilineal evolution theories. It emerged in the 1930s and extensively developed in the period following the Second World War and was incorporated into both anthropology and sociology in the 1960s. It bases its theories on empirical evidence from areas of archaeology, palaeontology and historiography and tries to eliminate any references to systems of values, be it moral or cultural, instead trying to remain objective and simply descriptive.

While 19th-century evolutionism explained how culture develops by giving general principles of its evolutionary process, it was dismissed by the Historical Particularists as unscientific in the early 20th century. It was the neoevolutionary thinkers who brought back evolutionary thought and developed it to be acceptable to contemporary anthropology.

Neoevolutionism discards many ideas of classical social evolutionism, namely that of social progress, so dominant in previous sociology evolution-related theories. Then neoevolutionism discards the determinism argument and introduces probability, arguing that accidents and free will greatly affect the process of social evolution. It also supports counterfactual history—asking "what if" and considering different possible paths that social evolution may take or might have taken and thus allows for the fact that various cultures may develop in different ways, some skipping entire stages others have passed through. Neoevolutionism stresses the importance of empirical evidence. While 19th-century evolutionism used value judgments and assumptions for interpreting data, neoevolutionism relied on measurable information for analysing the process of sociocultural evolution.

Leslie White, author of *The Evolution of Culture: The Development of Civilization to the Fall of Rome* (1959), attempted to create a theory explaining the entire history of humanity. The most important factor in his theory is technology. *Social systems are determined by technological systems*, wrote White in his book, echoing the earlier theory of Lewis Henry Morgan. He proposes a society's energy consumption as a measure of its advancement. He differentiates between five stages of human development. In the first, people use the energy of their own muscles. In the second, they use the energy of domesticated animals. In the third, they use the energy of plants (so White refers to agricultural revolution here). In the fourth, they learn to use the energy of natural resources: coal, oil, gas. In the fifth, they harness nuclear energy. White introduced a formula, P=E*T, where E is a measure of energy consumed and T is the measure of efficiency of technical factors utilising the energy. This theory is similar to Russian astronomer Nikolai Kardashev's later theory of the Kardashev scale.

Julian Steward, author of *Theory of Culture Change: The Methodology of Multilinear Evolution* (1955, reprinted 1979), created the theory of "multilinear" evolution which examined the way in which societies adapted to their environment. This approach was more nuanced than White's theory of "unilinear evolution." Steward rejected the 19th-century notion of progress and instead called attention to the Darwinian notion of "adaptation", arguing that all societies had to adapt to their environment in some way. He argued that different adaptations could be studied through the examination of the specific resources a society exploited, the technology the society relied on to exploit these resources and the organization of human labour. He further argued that different environments and technologies would require different kinds of adaptations and that as the resource base or technology changed, so too would a culture. In other words, cultures do not change according to some inner logic, but rather in terms of a changing relationship with a changing environment. Cultures therefore would not pass through the same stages in the same order as they changed—rather, they would change in varying ways and directions. He called his theory "multilineal evolution". He questioned the possibility of creating a social theory encompassing the entire evolution of humanity; however, he argued that anthropologists are not limited to describing specific existing cultures. He believed that it is possible to create theories analysing typical common culture, representative of specific eras or regions. As the decisive factors determining the development of given culture he pointed to technology and economics, but noted that there are secondary factors, like political system, ideologies and religion. All those factors push the evolution of a given society in several directions at the same time; hence the application of the term "multilinear" to his theory of evolution.

Marshall Sahlins, co-editor with Elman Service of *Evolution and Culture* (1960), divided the evolution of societies into 'general' and 'specific'. General evolution is the tendency of cultural and social systems to increase in complexity, organization and adaptiveness to environment. However, as the various cultures are not isolated, there is interaction and a diffusion of their qualities (like technological inventions). This leads cultures to develop in different ways (specific evolution), as various elements are introduced to them in different combinations and at different stages of evolution.

In his *Power and Prestige* (1966) and *Human Societies: An Introduction to Macrosociology* (1974), Gerhard Lenski expands on the works of Leslie White and Lewis Henry Morgan. He views technological progress as the most basic factor in the evolution of societies and cultures. Unlike White, who defined technology as the ability to create and utilise energy, Lenski focuses on information—its amount and uses. The more information and knowledge (especially allowing the shaping of natural environment) a given society has, the more advanced it is. He distinguishes four stages of human development, based on advances in the history of communication. In the first stage, information is passed by genes. In the second, when humans gain sentience, they can learn and pass information through by experience. In the third, humans start using signs and develop logic. In the fourth, they can create symbols and develop language and writing. Advancements in the technology of communication translate into advancements in the economic system and political system, distribution of goods, social inequality and other spheres of social life. He also differentiates societies based on their level of technology, communication and economy: (1) hunters and gatherers, (2) agricultural, (3) industrial and (4) special (like fishing societies).

Talcott Parsons, author of *Societies: Evolutionary and Comparative Perspectives* (1966) and *The System of Modern Societies* (1971) divided evolution into four subprocesses: (1) division, which creates functional subsystems from the main system; (2) adaptation, where those systems evolve into more efficient versions; (3) inclusion of elements previously excluded from the given systems; and (4) generalization of values, increasing the legitimization of the ever more complex system. He shows those processes on 4 stages of evolution: (I) primitive or foraging, (II) archaic agricultural, (III) classical or "historic" in his terminology, using formalized and universalizing theories about reality and (IV) modern empirical cultures. However, these divisions in Parsons theory is the more formal ways in which the evolutionary process is conceptualized and should not be mistaken for with Parsons' actual theory. Parsons develops a theory, where he tries to reveal the complexity of the processes which take form between two points of necessity, the first is the cultural "necessity," which is given through the values-system of each evolving community; the other is the environmental necessities, which most directly is reflected in the material realities of the basic production system and reflected in the relative capacity of each industrial-economical level at each window of time. Generally, Parsons highlights that the dynamics and directions of these process is shaped by the cultural imperative embodied in the cultural heritage and more secondary an outcome of sheer "economic" conditions.

Sociobiology

Sociobiology departs perhaps the furthest from classical social evolutionism. It was introduced by Edward Wilson in his 1975 book *Sociobiology: The New Synthesis* and followed his adaptation of evolutionary theory to the field of social sciences. Wilson pioneered the attempt to explain the evolutionary mechanics behind social behaviours such as altruism, aggression and nurturance. In doing so, Wilson sparked one of the greatest scientific controversies of the 20th century.

Sociobiologists have argued for a dual inheritance theory, which posits that humans are products of both biological evolution and sociocultural evolution, each subject to their own selective mechanisms and forms of transmission (i.e. in the case of biology, genes and cultural evolutionary units are often called memes). This approach focuses on both the mechanisms of cultural transmission and the selective pressures that influence cultural change. This version of sociocultural evolution shares little in common with the stadial evolutionary models of the early and mid-20th century. This approach has been embraced by many psychologists and some cultural anthropologists, but very few physical anthropologists.

The current theory of evolution, the modern evolutionary synthesis (or neo-darwinism), explains that evolution of species occurs through a combination of Darwin's mechanism of natural selection and Gregor Mendel's theory of genetics as the basis for biological inheritance and mathematical population genetics. Essentially, the modern synthesis introduced the connection between two important discoveries; the units of evolution (genes) with the main mechanism of evolution (selection).

Due to its close reliance on biology, sociobiology is often considered a branch of the biology and sociology disciplines, although it uses techniques from a plethora of sciences, including ethology, evolution, zoology, archaeology, population genetics and many others. Within the study of human societies, sociobiology is closely related to the fields of human behavioral ecology and evolutionary psychology.

Sociobiology has remained highly controversial as it contends genes explain specific human behaviours, although sociobiologists describe this role as a very complex and often unpredictable interaction between nature and nurture. The most notable critics of the view that genes play a direct role in human behaviour have been biologists Richard Lewontin and Stephen Jay Gould.

Since the rise of evolutionary psychology, another school of thought, Dual Inheritance Theory, has emerged in the past 25 years that applies the mathematical standards of Population genetics to modeling the adaptive and selective principles of culture. This school of thought was pioneered by Robert Boyd at UCLA and Peter Richerson at UC Davis and expanded by William Wimsatt, among others. Boyd and Richerson's book, *Culture and the Evolutionary Process* (1985), was a highly mathematical description of cultural change, later published in a more accessible form in *Not by Genes Alone* (2004). In Boyd and Richerson's view, cultural evolution, operating on socially learned information, exists on a separate ground from genetic evolution and while the two are related, cultural evolution is more dynamic, rapid and influential on human society than genetic evolution.

Theory of modernization

Theories of modernization have been developed and popularized in 1950s and 1960s and are closely related to the dependency theory and development theory. They combine the previous theories of sociocultural evolution with practical experiences and empirical research, especially those from the era of decolonization. The theory states that:

- Western countries are the most developed and rest of the world (mostly former colonies) are on the earlier stages of development and will eventually reach the same level as the Western world.
- Development stages go from the traditional societies to developed ones.
- Third World countries have fallen behind with their social progress and need to be directed on their way to becoming more advanced.

Developing from classical social evolutionism theories, theory of modernization stresses the modernization factor: many societies are simply trying (or need to) emulate the most successful societies and cultures. It also states that it is possible to do so, thus supporting the concepts of social engineering and that the developed countries can and should help those less developed, directly or indirectly.

Among the scientists who contributed much to this theory are Walt Rostow, who in his *The Stages of Economic Growth: A Non-Communist Manifesto* (1960) concentrates on the economic system side of the modernization, trying to show factors needed for a country to reach the path to modernization in his Rostovian take-off model. David Apter concentrated on the political system and history of democracy, researching the connection between democracy, good governance and efficiency and modernization. David McClelland (*The Achieving Society*, 1967) approached this subject from the psychological perspective, with his motivations theory, arguing that modernization cannot happen until given society values innovation, success and free enterprise. Alex Inkeles (*Becoming Modern*, 1974) similarly creates a model of *modern personality*, which needs to be independent, active, interested in public policies and cultural matters, open for new experiences, rational and being able to create long-term plans for the future. Some works of Jürgen Habermas are also connected with this subfield.

Theory of modernization has been subject to some criticism similar to that levied on classical social evolutionism, especially for being too ethnocentric, one-sided and focused on the Western world and culture.

Prediction for a stable cultural and social future

Cultural evolution follows punctuated equilibrium which Gould and Eldredge developed for biological evolution. Bloomfield has written that human societies follow punctuated equilibrium which would mean first, a stable society, a transition resulting in a subsequent stable society with greater complexity. Using these guidelines, mankind has had a stable animal society, a transition to a stable tribal society, another transition to a stable peasant society and is currently in a transitional industrial society.

The status of a human society rests on the productivity of food production. Deevey reported on the growth of the number of humans. Deevey also reported on the productivity of food production, noting that productivity changes very little for stable societies, but increases during transitions. When productivity and especially food productivity can no longer be increased, Bloomfield has proposed that man will have achieved a stable automated society. Space is also assumed to allow for the continued growth of the human population, as well as provide a solution to the current pollution problem by providing limitless energy from solar satellite power stations.

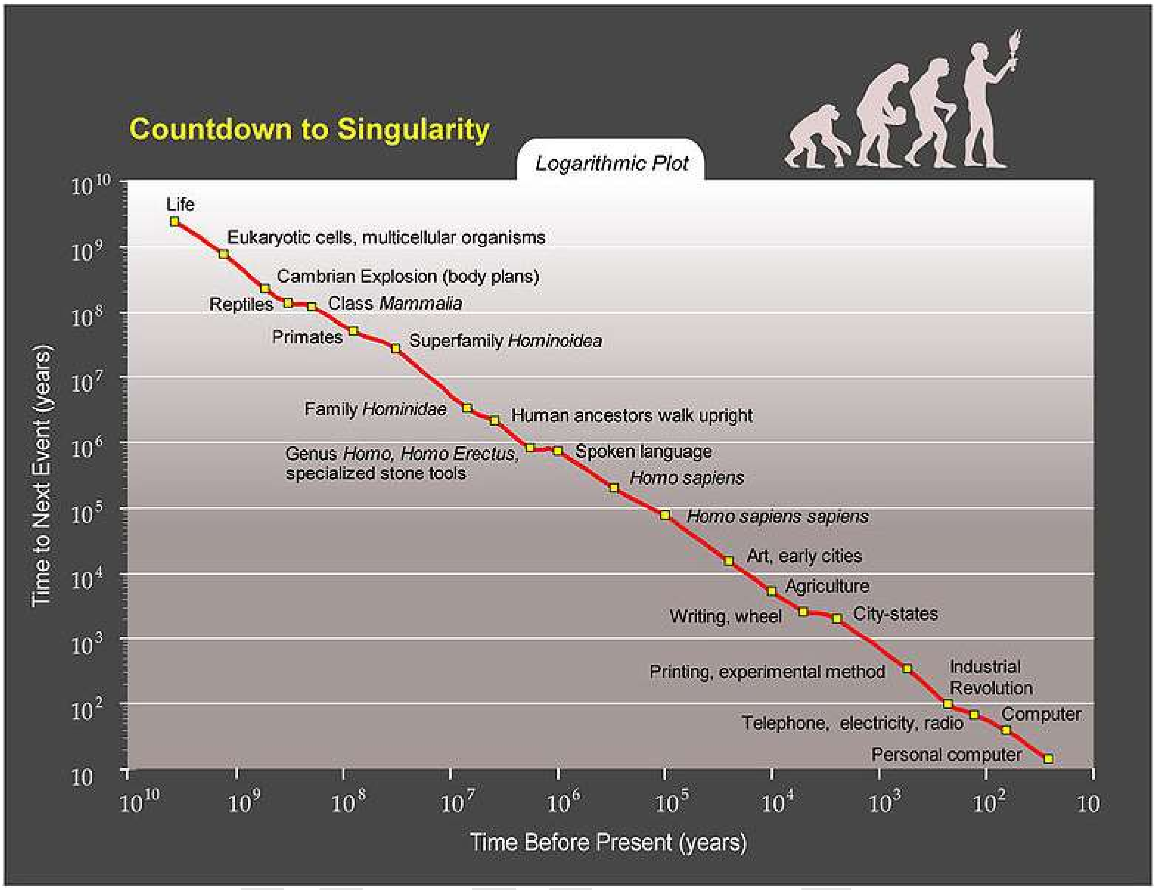
Theory of postindustrial society

Scientists have used the theory of evolution to analyze various trends and to predict the future development of societies. These scientists have created the theories of postindustrial societies, arguing that the current era of industrial society is coming to an end and services and information are becoming more important than industry and goods.

In 1974, sociologist Daniel Bell, author of *The Coming of Post-Industrial Society*, introduced the concept of postindustrial society. He divided the history of humanity into three eras: pre-industrial, industrial and postindustrial. He predicted that by the end of the 20th century, United States, Japan and Western Europe would reach the postindustrial stage. This "post-industrial" stage would be demonstrated by:

- domination of the service sector (administration, banking, trade, transport, healthcare, education, science, mass media, culture) over the traditional industry sector (manufacturing industries, which have surpassed the more traditional, agriculture and mining sector after the 19th-century Industrial Revolution);
- growing importance of information technologies;
- increased role of long-term planning, modelling future trends;
- domination of technocracy and pragmatism over traditional ethics and ideologies;
- increasing importance and use of technology and intellect;
- changes in the traditional hierarchy of social classes, with highly educated specialists and scientists overtaking the traditional bourgeois;

From the 1970s many other sociologists and anthropologists, like Alvin Toffler (*Future Shock*, 1970) and John Naisbitt (*Megatrends 2000: The New Directions for the 1990s*, 1982) have followed in Bell's footsteps and created similar theories. John Naisbitt introduced the concept of megatrends: powerful, global trends that are changing societies on the worldwide scale. Among the megatrends that he mentions was the process of globalization. Another important megatrend was the increase in performance of computers and the development of the World Wide Web. Marshall McLuhan introduced the concept of the global village (*The Gutenberg Galaxy*, 1962) and this term was soon adapted by the researchers of globalization and the Internet. Naisbitt and many other proponents of the theory of postindustrial societies argues that those megatrends lead to decentralization, weakening of the central government, increasing importance of local initiatives and direct democracy, changes in the hierarchy of the traditional social classes, development of new social movements and increased powers of consumers and number of choices available to them (Toffler even used the term "overchoice").



Logarithmic plot, according to Ray Kurzweil showing an exponential shortening trend in evolution of humanity, basis for the technological singularity theory.

Some of the more extreme visions of the postindustrial society are those related to the theory of the technological singularity. This theory refers to a predicted point or period in the development of a civilization at which due to the acceleration of technological progress, the societal, scientific and economic change is so rapid that nothing beyond that time can be reliably comprehended, understood or predicted by the pre-Singularity humans. Such a singularity was first discussed in the 1950s and vastly popularized in the 1980s by Vernor Vinge.

Critics of the postindustrial society theory point out that it is very vague and as any prediction, there is no guarantee that any of the trends visible today will in fact exist in the future or develop in the directions predicted by contemporary researchers. However, no serious sociologist would argue it is possible to predict the future, but only that such theories allow us to gain a better understanding of the changes taking place in the modernised world.

Contemporary discourse over sociocultural evolution

The Cold War period was marked by rivalry between two superpowers, both of which considered themselves to be the most highly evolved cultures on the planet. The USSR painted itself as a socialist society which emerged out of class struggle, destined to reach the state of communism, while sociologists in the United States (such as Talcott Parsons) argued that the freedom and prosperity of the United States were a proof of a higher level of sociocultural evolution of its culture and society. At the same time, decolonization created newly independent countries who sought to become more developed—a model of progress and industrialization which was itself a form of sociocultural evolution.

There is, however, a tradition in European social theory from Rousseau to Max Weber that argues that this progression coincides with a loss of human freedom and dignity. At the height of the Cold War, this tradition merged with an interest in ecology to influence an activist culture in the 1960s. This movement produced a variety of political and philosophical programs which emphasised the importance of bringing society and the environment into harmony.

Current political theories of the new tribalists consciously mimic ecology and the life-ways of indigenous peoples, augmenting them with modern sciences. Ecoregional Democracy attempts to confine the "shifting groups", or tribes, within "more or less clear boundaries" that a society inherits from the surrounding ecology, to the borders of a naturally occurring ecoregion.

Progress can proceed by competition between but not within tribes and it is limited by ecological borders or by Natural Capitalism incentives which attempt to mimic the pressure of natural selection on a human society by forcing it to adapt consciously to scarce energy or materials. Gaians argue that societies evolve deterministically to play a role in the ecology of their biosphere, or else die off as failures due to competition from more efficient societies exploiting nature's leverage.

Thus, some have appealed to theories of sociocultural evolution to assert that optimising the ecology and the social harmony of closely knit groups is more desirable or necessary than the progression to "civilization." A 2002 poll of experts on Nearctic and Neotropic indigenous peoples (reported in *Harper's* magazine) revealed that *all of them* would have preferred to be a typical New World person in the year 1491, prior to any European contact, rather than a typical European of that time.

This approach has been criticised by pointing out that there are a number of historical examples of indigenous peoples doing severe environmental damage (such as the deforestation of Easter Island and the extinction of mammoths in North America) and that proponents of the goal have been trapped by the European stereotype of the noble savage.

Today, postmodernists question whether the notions of evolution or society have inherent meaning and whether they reveal more about the person doing the description than the thing being described. Observing and observed cultures may lack sufficient cultural similarities (such as a common foundation ontology) to be able to communicate their respective priorities easily. Or, one may impose such a system of belief and judgment upon another, via conquest or colonization. For instance, observation of very different ideas of mathematics and physics in indigenous peoples led indirectly to ideas such as George Lakoff's "cognitive science of mathematics", which asks if measurement systems themselves can be objective.

Chapter- 5

Denisova Hominin

The **Denisova hominin** is the name given to the remains of a member of the genus *Homo* that may be a previously unknown species based on an analysis of its mitochondrial DNA (mtDNA). In March 2010, discovery was announced of bone fragments of a juvenile that lived about 41,000 years ago found in Denisova Cave (Altai Krai, Russia), a region also inhabited at about the same time by Neanderthals and modern humans. The mtDNA of the Denisova hominin is distinct from the mtDNAs of Neanderthals and modern humans. In December 2010, an international team of scientists determined the sequence from the nuclear genome of this group (known as the **Denisovans**) from this finger bone. According to their analysis, this group shares a common origin with the Neanderthals and interbred with the ancestors of modern Melanesians.

Anatomy and lineage

Little is known of the precise anatomical features of the Denisovans since the only physical remains discovered thus far are the finger bone from which only mitochondrial genetic material was gathered. A tooth found in Denisova Cave carries a mtDNA very similar to that of the finger bone and shares no derived morphological features with Neanderthal or modern humans. The Siberian bone's mtDNA differs from that of modern humans by 385 bases (nucleotides) in the mtDNA strand out of approximately 16,500, whereas the difference between modern humans and Neanderthals is around 202 bases. In contrast, the difference between chimpanzees and modern humans is approximately 1,462 mtDNA base pairs. Analysis of the specimen's genome shows it to be due to a common branch of ancestors with Neanderthal lineage, but, after they diverged from one another, Denisovans and Neanderthals had largely separated population histories.

Discovery

In 2008, Russian archeologists working at the site of Denisova Cave in the Altai Mountains of Siberia uncovered a small bone fragment from the fifth finger of a juvenile hominin, dubbed the "X-woman" (referring to the maternal descent of mitochondrial DNA), or the Denisova hominin. Artifacts, including a bracelet, excavated in the cave at the same level were carbon dated to around 40,000 BP.

A team of scientists led by Johannes Krause and Swedish biologist Svante Pääbo from the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, sequenced mtDNA extracted from the fragment. Because of the cool climate in the location of the Denisova Cave, the discovery benefited from DNA's ability to survive for longer periods at lower temperatures. The analysis indicated that modern humans, Neanderthals and the Denisova hominin last shared a common ancestor around 1 million years ago. Some studies suggest that modern humans coexisted with Neanderthals in Europe and the discovery raises the possibility that Neanderthals, modern humans and the Denisovan hominin may have co-existed.

The DNA analysis further indicated that this new hominin species was the result of an early migration out of Africa, distinct from the later out-of-Africa migrations associated with Neanderthals and modern humans, but also distinct from the earlier African exodus of *Homo erectus*. Professor Chris Stringer, human origins researcher at London's Natural History Museum and one of the leading proponents of the recent single-origin hypothesis, remarked: "This new DNA work provides an entirely new way of looking at the still poorly understood evolution of humans in central and eastern Asia." Pääbo noted that the existence of this distant branch creates a much more complex picture of humankind during the Late Pleistocene.

In 2010, a second paper from the Svante Pääbo group reported the prior discovery, in 2000, of a third upper molar from a young adult, dating from about the same time (the finger was from level 11 in the cave sequence, the tooth from level 11.1). The tooth differed in several aspects from those of Neanderthals while having archaic characteristics similar to the teeth of *Homo erectus*. They again performed mitochondrial DNA analysis on the tooth and found it to have a different but similar sequence to that of the finger bone, indicating a divergence time about 7,500 years before and suggesting it belonged to a different individual from the same population.

Nuclear genome analysis

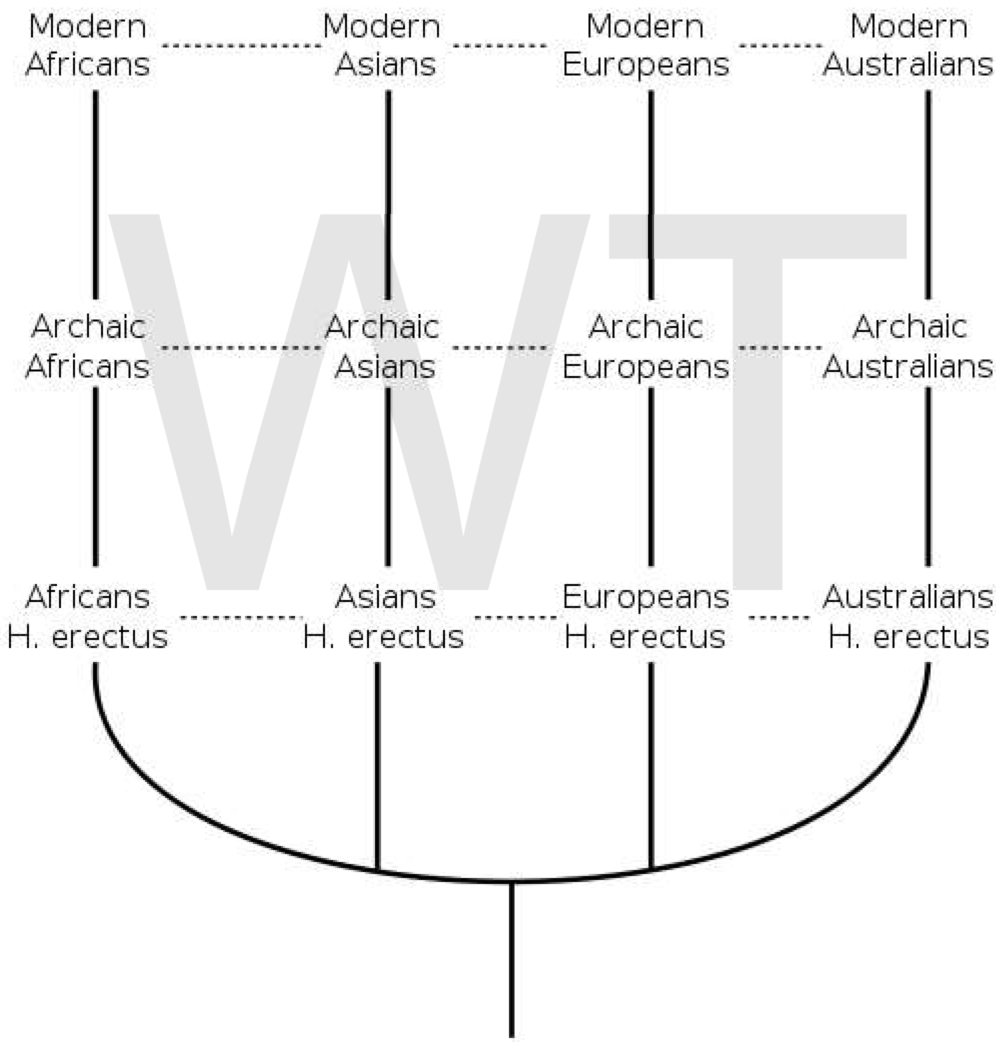
In the same 2010 paper, the authors report the isolation and sequencing of nuclear DNA from the Denisova finger bone. This specimen showed an unusual degree of DNA preservation and low level of contamination. They were able to achieve near-complete genomic sequencing, allowing a detailed comparison with Neanderthal and modern humans. From this analysis, they concluded that in spite of the apparent divergence of their mitochondrial sequence, the Denisova population along with Neanderthal shared a common branch from the lineage leading to modern African humans. The estimated time of divergence between Denisovans and Neanderthals is 640,000 years ago and that between both these groups and modern Africans is 804,000 years ago. They suggest that the divergence of the Denisova mtDNA results either from the persistence of a lineage purged from the other branches of humanity through genetic drift or else an introgression from an older hominin lineage.

Interbreeding with modern humans

In addition to genetic studies linking approximately 4% of non-African modern human DNA to Neanderthals, these tests comparing the Denisova hominin genome with those of six modern humans whose genome has been sequenced, a !Kung from South Africa, a Nigerian, a French person, a Papua New Guinean, a Bougainville Islander and a Han Chinese showed that between 4% and 6% of the genome of Melanesians (represented by the Papua New Guinean and Bougainville Islander) derives from a Denisovan population, possibly introduced during the early migration of the ancestors of Melanesians into Southeast Asia. This history of interaction suggests that Denisovans once ranged widely over eastern Asia.

Chapter- 6

Multiregional Origin of Modern Humans



A graph detailing the evolution to modern humans using the Multiregional theory of human evolution. The horizontal lines represent 'multiregional evolution' gene flow between regional lineages.

The **multiregional hypothesis** is a scientific model that provides an explanation for the pattern of human evolution. The hypothesis holds that the evolution of humanity from near the beginning of the Pleistocene two million years ago to the present day has been within a single, continuous human species. This species encompasses archaic human forms such as *Homo erectus* and Neanderthals as well as modern forms, which are held to be subspecies and evolved worldwide to the diverse populations of modern *Homo sapiens sapiens*. The theory contends that there was some human genetic continuity in various regions of the world as well as gene interchange between the regions. Proponents of multiregional origin point to fossil and genomic evidence as support for their hypothesis.

The primary competing hypothesis is recent African origin of modern humans (also known as "Out of Africa"), which contends that modern humans arose in Africa around 100-200,000 years ago, moving out of Africa around 50-60,000 years ago to replace the other human forms without interbreeding.

Regional continuity

The term "multiregional hypothesis" was first coined in the early 1980s by Milford H. Wolpoff and colleagues as an explanation for the apparent similarities seen in *Homo erectus* and *Homo sapiens* fossils from the same region, what they called *regional continuity*.

Wolpoff rejected the earlier proposal by Coon of parallel evolution and proposed a theory based on clinal variation that would allow for the necessary balance between local selection and a global species. He proposed that *Homo erectus*, Neanderthals, *Homo sapiens* and other humans were a single species. This species arose in Africa two million years ago as *H. erectus* and then spread out over the world, developing adaptations to regional conditions. It was proposed that for periods of time some populations became isolated, developing in a different direction, but through continuous interbreeding, replacement, genetic drift and selection, adaptations that were an advantage anywhere on earth would spread, keeping the development of the species in the same overall direction, while maintaining adaptations to regional factors. Eventually, the more unusual local varieties of the species would have disappeared in favor of modern humans, retaining some regional adaptations, but with many common features.

Fossil evidence

Replica of Sangiran 17 *Homo erectus* skull from Indonesia showing obtuse face to vault angle determined by fitting of bones at brow

Cast of anatomically modern human Kow Swamp 1 skull from Australia with a face to vault angle matching that of Sangiran 17

Proponents of the multiregional hypothesis see regional continuity of certain morphological traits from archaic humans to modern humans, demonstrating regional genetic continuity, even as changes in other traits occur in parallel over time across all regions, demonstrating lateral genetic exchange. For example, in 2001 Wolpoff and colleagues published an analysis of character traits of the skulls of early modern human fossils in Australia and central Europe. They concluded that the diversity of these recent humans could not "result exclusively from a single late Pleistocene dispersal" and implied dual ancestry from Javan *Homo erectus* for Australia and from Neanderthals for Central Europe.

Southeast Asia

Alan Thorne held that there was regional continuity in the human fossils in southeast Asia. Wolpoff, initially skeptical, became convinced when reconstructing the Sangiran 17 *Homo erectus* skull from Indonesia, when he was surprised that the skull's face to vault angle matched that of the Australian modern human Kow Swamp 1 skull. Wolpoff had expected the skull to match that of the *Homo erectus* specimens from China like the Dali skull, but instead, the face to vault angle seemed to be retained regionally over time, even while the fossils in the two regions showed parallel increases in brain case size and parallel reductions in masticatory structures over the intervening approximately 750,000 years.

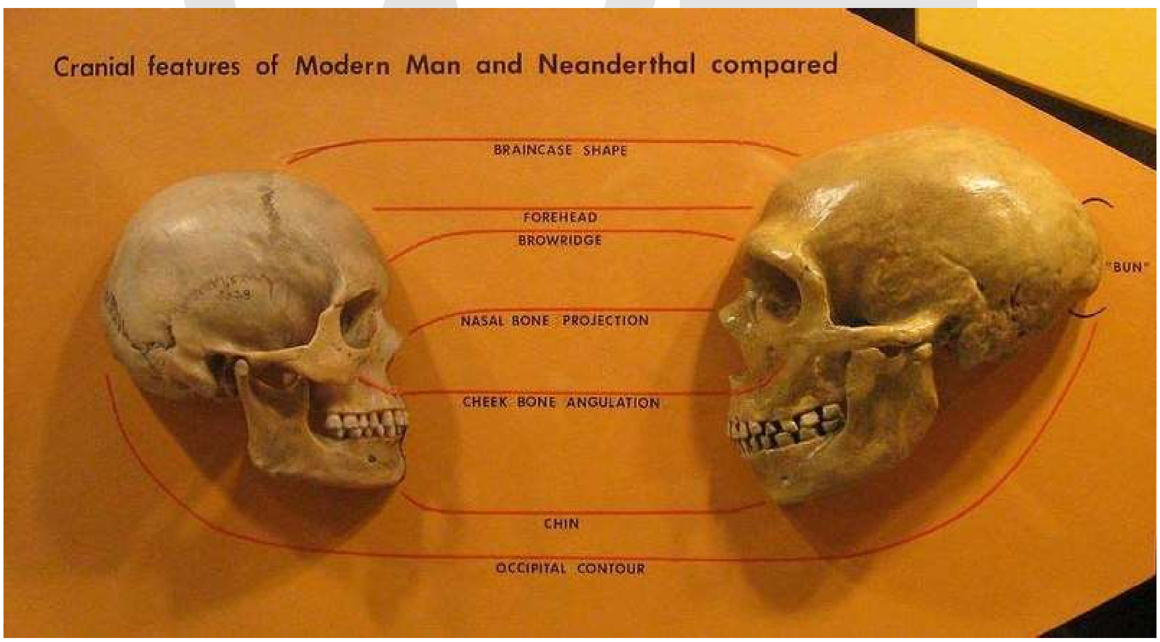
China

Replica of *Homo erectus* ("Peking man") skull from China

Franz Weidenreich, who oversaw the excavations of numerous "Peking man" *Homo erectus* fossils at Zhoukoudian in the early 20th century, believed the fossil record demonstrated certain unique features linking prehistoric and modern human populations in China. Many subsequent Chinese paleoanthropologists, such as Wu Xinzhi, were also disposed to favor the multiregional hypothesis for the same reason.

More recent finds provide additional support for regional human continuity in China. The *Tianyuan 1* specimen unearthed in 2003 in Tianyuan Cave, Zhoukoudian and Carbon 14 dated to 42-39 kya exhibits a series of typical modern human features such as a distinct chin. However, the skeleton also has archaic traits such as low anterior to posterior dental proportions indicating relatively large molars and certain leg bone proportions typical of archaic forms such as Neanderthals. Shang *et. al.* conclude that this combination of modern and archaic traits "implies that a simple spread of modern humans from Africa is unlikely." A jaw bone found in 2008 and dated to 110,000 kya may also exhibit a mixture of archaic and modern human traits.

Europe



Comparison of modern human and neanderthal skull

Proponents of the multiregional hypothesis argue for regional continuity in Europe on the basis of skeletal anatomy, morphology and genetics of speech and the archaeology of the middle to upper paleolithic transition, which they believe to be inconsistent with the possibility of complete replacement of the Neanderthals in Europe without interbreeding.

Some detractors of the theory have argued, in contrast, that the morphological differences between Neanderthals and early and modern humans indicate that they are different species, based on skull differences more distinct than between any subspecies pairs examined except for the two subspecies of gorilla, implying limited or no interbreeding.

Many of the multiregional claims regarding skeletal morphology in Europe center on forms with both archaic Neanderthal traits and modern traits, to provide evidence of interbreeding rather than replacement. Examples include the *Lapedo child* found in Portugal and the *Oase 1* mandible from Peştera cu Oase, Romania, though the *Lapedo child* example is disputed by some. In a 2007 paper examining numerous samples from European early modern humans, later European humans from the Gravettian period and the earlier Neanderthal and east African populations from whom the first two populations could have descended, Erik Trikaus identified numerous features in the later European samples which were absent from the African sample, but present in the Neanderthal sample. These features included various aspects of skull and mandible shape, tooth shape and size and shapes and proportions of other bones. Trinkaus concluded that early modern Europeans had predominant African ancestry with a substantial degree of admixture from the Neanderthals then indigenous to Europe.

Genetic evidence

Genetic evidence from the late 1980s on the mitochondrial genome indicated that all living humans had as an ancestor a single female living in African about 200,000 years ago. This led to a hypothesis that around that time period, a small founder population of humans left Africa and eventually replaced all archaic humans then living outside of Africa without interbreeding, contrary to the multiregional hypothesis. However, as data on the far larger autosomal DNA genome started to became available, evidence mounted that genetic contributions from archaic human populations from around the world and not just from Africa, also persist in modern humans. Recent analyses of DNA taken directly from Neanderthal and denisovan specimens indicates that those populations also contributed to the genome of living humans, as predicted by the multiregional hypothesis.

Mitochondrial DNA

A 1987 analysis of mitochondrial DNA from 147 people from around the world indicated that their mitochondrial lineages all traced to a common ancestor in Africa about 200,000 years ago. The analysis suggested that this reflected the worldwide expansion of modern humans as a new species, replacing rather than mixing with local archaic humans. Later analysis of mitochondrial DNA from neanderthals and from the denisova hominin indicated that those mitochondrial strains had diverged from the living human mitochondrial line long before 200,000 years ago, consistent with lack of interbreeding between early modern and archaic humans.

The original mitochondrial DNA results and the resulting recent African replacement theory posed a serious challenge to the multiregional hypothesis. Mitochondrial DNA alone, however, could not entirely rule out interbreeding between early modern and archaic humans, since archaic human mitochondrial strains from such interbreeding could have been lost due to genetic drift. Indeed, later analysis of autosomal DNA from both modern and archaic humans was to show results very different from those from mitochondrial DNA.

Autosomal and X chromosome DNA

By analysing haplotype data, Alan Templeton found support for three waves of human migration out of Africa, the first being 1.9 million years ago and concluded that it was impossible that existing Eurasian populations had not interbred with African migrants.

Studies on past population bottlenecks that can be inferred from molecular data have led multiregionalists to conclude that the recent single-origin hypothesis is untenable because there are no population size bottlenecks affecting all genes that are more recent than 2 million years ago.

- CMAH CMP-N-acetylneuraminic acid hydroxylase pseudogene show 2.9 Mya coalescence time.
- NAT2 SNPs lineages cluster in sub-Saharan Africa, Europe and East Asia, with genetic distances scaling with geographic distances. The NAT1 lineage tree is rooted in Eurasia with a coalescence time of 2.0 Mya that cannot be explained by balancing selection and the NAT1*11A haplotype absent from subsaharan Africa.
- ALMS1 suggest ancient and complex evolutionary history with a coalescence time of about 2 Mya.
- Analyses of a region of RRM2P4 (ribonucleotide reductase M2 subunit pseudogene 4) showed a coalescence time of about 2 Mya, with a clear root in Asia.
- PDHA1 (pyruvate dehydrogenase) locus on X chromosome has estimated coalescent-time depth of 1.86 Ma, although the worldwide lineage pattern is unlike other autosomal sites and consistent with recent dispersal from Africa.
- MAPT locus 17q21.3 split into deep genetic lineages H1 and H2. H2 lineage in European population suggest inheritance from Neanderthals.
- ASAH1. Related to mental activity N-Acylsphingosine Amidohydrolase gene two V and M deep genetic lineages have TMRCA 2.4±.4 Ma. Linkage disequilibrium 62% and small nucleotide diversity 0.05% indicate a signature of positive Darwinian selection for the V lineage. The M lineage is attributed to ancient population structure of humans in Africa.
- X-chromosome genes DMD44, APXL, AMELX, TNFSF5 show S-N heterogeneous patterns of variation. While these genes do show the greatest diversity in Africa, consistent with recent African replacement, the genes' varying

diversity by region cannot be explained by simple expansion from Africa, which should have resulted in similar diversity patterns for all these genes.

- Genome polymorphism: Inversion polymorphism: known 5-million-base pair (Mbp) 8p23.1, 1-Mbp on 17q21.3 and novel 1.2-Mbp on 15q24, 2.1-Mbp 15q13, 1.7-Mbp 17q12. In the sample of 8 gnomes from worldwide sample including Yuruba Kidd&al group found 4 million SNPs and 796,273 small indels (1−100 bp in size); 15 large regions of excess nucleotide variation 500 kbp to 3 Mbp. Two of variable sites are described detailed above.

- Microcephalin D allele introgressed into the modern human gene pool points to the Neanderthal lineage as possible source and compelling evidence of admixture among the human loci.

Proponents of the multiregional hypothesis show genetic sequences of several loci in the human genome with million year old genealogy. Those data of deep genetic lineages are explained in the multiregional theory framework as a result of heredity from *structured ancestral population*. The data are not interpreted in light of the RAO hypothesis postulating recent replacement where separated million years ago genetic lineages are at best unpredicted.

DNA from archaic humans

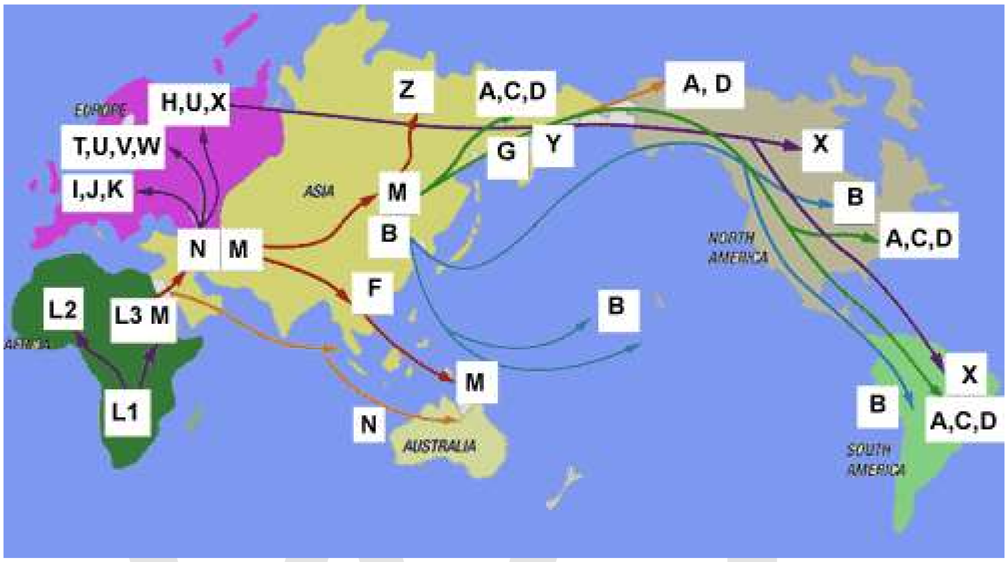
By 2006, extraction of DNA directly from some archaic human samples was becoming possible. The earliest analyses were of neanderthal DNA and indicated that the neanderthal contribution to modern human genetic diversity was no more than 20%, with a most likely value of 0%. By 2010, however, detailed DNA sequencing of the neanderthal specimens from Europe indicated that the contribution was nonzero, with neanderthals sharing 1-4% more genetic variants with living nonafricans than with living humans in subsaharan Africa, supporting regional continuity outside of Africa. In late 2010, a recently discovered nonneanderthal archaic human, the denisova hominin from southern siberia, was found to share 4-6% of its genome with living melanesian humans and with no other living group, supporting lateral gene transfer between two regions outside of Africa. The combination of regional continuity inside and outside of Africa and lateral gene transfer between various regions around the world supports the multiregional hypothesis.

Alternate hypotheses

Polygenism

The polygenic hypothesis for human origins, popular in the 19th and early 20th centuries, proposed that human populations had evolved independently and in parallel in the various regions of the world, without gene interchange. This differs from multiregional evolution in that the multiregional model posits significant lateral gene flow through migrations or interbreeding between populations, while polygenism envisions none. The polygenic hypothesis is no longer considered a viable scientific hypothesis since separately evolving species could not develop the interfertility of modern human populations.

Recent African replacement



Map of early human migrations according to mitochondrial population genetics

In paleoanthropology, the **recent African origin of modern humans** is the mainstream model describing the origin and early dispersal of anatomically modern humans. The theory is called the *(Recent) Out-of-Africa* model in the popular press and academically the *recent single-origin hypothesis* (*RSOH*), *Replacement Hypothesis* and *Recent African Origin* (*RAO*) model. The hypothesis that humans have a single origin (monogenesis) was published in Charles Darwin's *Descent of Man* (1871). The concept was speculative until the 1980s, when it was corroborated by a study of present-day mitochondrial DNA, combined with evidence based on physical anthropology of archaic specimens. According to genetic and fossil evidence, archaic *Homo sapiens* evolved to anatomically modern humans solely in Africa, between 200,000 and 100,000 years ago, with members of one branch leaving Africa by 60,000 years ago and over time replacing earlier human populations such as Neanderthals and *Homo erectus*.

The recent single origin of modern humans in East Africa was the near-consensus position held within the scientific community until 2010. However, recent sequencing of autosomal DNA from neanderthals and from an archaic human from denisova suggest that these populations, which were already outside of Africa at the posited time of the recent African human origin, also contributed to the modern human gene pool.

The competing hypothesis is the multiregional origin of modern humans. Some push back the original "out of Africa" migration—in this case, by *Homo erectus*, not by *Homo sapiens*—to two million years ago.

History of the theory

With the development of anthropology in the early 19th century, scholars disagreed vigorously about different theories of human development. Those such as Johann Friedrich Blumenbach and James Cowles Pritchard held that since the creation, the various human races had developed as different varieties sharing descent from one people (monogenism). Their opponents, such as Louis Agassiz and Josiah C. Nott, argued for polygenism, or the separate development of human races as separate species, or had developed as separate species through transmutation of species from apes, with no common ancestor.

Charles Darwin was one of the first to propose common descent of living organisms and among the first to suggest that all humans had in common ancestors who lived in Africa. In the *Descent of Man*, he speculated that humans had descended from apes which still had small brains but walked upright, freeing their hands for uses which favoured intelligence. Further, he thought such apes were African:

In each great region of the world the living mammals are closely related to the extinct species of the same region. It is, therefore, probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee; and as these two species are now man's nearest allies, it is somewhat more probable that our early progenitors lived on the African continent than elsewhere. But it is useless to speculate on this subject, for an ape nearly as large as a man, namely the Dryopithecus of Lartet, which was closely allied to the anthropomorphous Hylobates, existed in Europe during the Upper Miocene period; and since so remote a period the earth has certainly undergone many great revolutions and there has been ample time for migration on the largest scale.
—Charles Darwin, *Descent of Man*

The prediction was insightful because at the time, in 1871, there were hardly any human fossils of ancient hominids available. Almost fifty years later, Darwin's speculation was supported when anthropologists began finding numerous fossils of ancient small-brained hominids in several areas of Africa (list of hominina fossils).

The debate in anthropology had swung in favour of monogenism by the mid-20th century. Isolated proponents of polygenism held forth in the mid-20th century, such as Carleton Coon, who hypothesized as late as 1962 that *Homo sapiens* arose five separate times from *Homo erectus* in five separate places. The "Recent African origin" of modern humans means "single origin" (monogenism) and has been used in various contexts as an antonym to polygenism.

With the advent of archaeogenetics in the 1990s, scientists were able to date the "out of Africa" migration with some confidence. In 2000, the mitochondrial DNA (mtDNA) sequence of "Mungo Man" of ancient Australia was published. This work was later questioned and explained by W. James Peacock, leader of the team who sequenced Mungo man's ancient mtdna.

The question of whether there was inheritance of other typological (not *de facto*) *Homo* subspecies into the *Homo sapiens* genetic pool remains under debate.

Early Homo sapiens

Anatomically modern humans originated in Africa about 250,000 years ago. The trend in cranial expansion and the acheulean elaboration of stone tool technologies which occurred between 400,000 years ago and the second interglacial period in the Middle Pleistocene (around 250,000 years ago) provide evidence for a transition from *H. erectus* to *H. sapiens*. In the Recent African Origin (RAO) scenario, migration within and out of Africa eventually replaced the earlier dispersed *H. erectus*.

Homo sapiens idaltu, found at site Middle Awash in Ethiopia, lived about 160,000 years ago. It is the oldest known anatomically modern human and classified as an extinct subspecies. Fossils of early *Homo sapiens* were found in Qafzeh cave in Israel and have been dated to 80,000 to 100,000 years ago. However these humans seem to have either become extinct or retreated back to Africa 70,000 to 80,000 years ago, possibly replaced by south bound Neanderthals escaping the colder regions of ice age Europe. Hua Liu & al. analyzing autosomal microsatellite markers dates to c. 56,000±5,700 years ago mtDNA evidence. He interprets the paleontological fossil of early modern human from Qafzeh cave as an isolated early offshoot that retracted back to Africa.

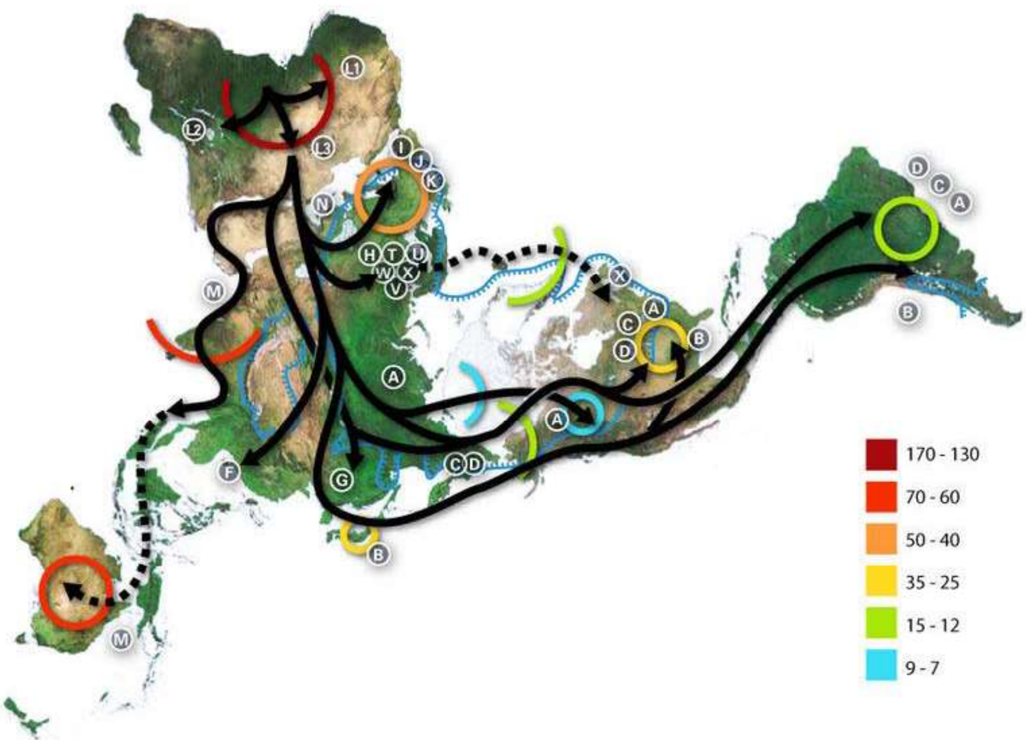
All other fossils of fully modern humans outside Africa have been dated to more recent times. The oldest well dated fossils found outside Africa are from Lake Mungo, Australia and have been dated to about 42,000 years ago. The Tianyuan cave remains in Liujiang region China have a probable date range between 38,000 and 42,000 years ago. They are most similar in morphology to Minatogawa Man, modern humans dated between 17,000 and 19,000 years ago and found on Okinawa Island, Japan. However, others have dated Liujang Man to 111,000 to 139,000 years before the present.

Beginning about 100,000 years ago evidence of more sophisticated technology and artwork begins to emerge and by 50,000 years ago fully modern behaviour becomes more prominent. By this time the ritual burying of the dead is noted. Stone tools show regular patterns that are reproduced or duplicated with more precision while tools made of bone and antler appear for the first time.

Genetic reconstruction

Two pieces of the human genome are quite useful in deciphering human history: mitochondrial DNA and the Y chromosome. These are the only two parts of the genome that are not shuffled about by the evolutionary mechanisms that generate diversity with each generation: instead, these elements are passed down intact. According to the hypothesis, all humans alive today inherited their mitochondria from one woman who lived in Africa about 160,000 years ago; she has been named Mitochondrial Eve. All men today have inherited their Y chromosomes from a man who lived 60,000 years ago, probably in Africa. He has been named Y-chromosomal Adam. It is now believed that more men participated in the out of Africa exodus of early humans than women based on comparing non-sex-specific chromosomes with sex-specific ones.

Mitochondrial DNA



One model of human migration based on Mitochondrial DNA

The first lineage to branch off from Mitochondrial Eve is L0. This haplogroup is found in high proportions among the San of Southern Africa, the Sandawe of East Africa. It is also found among the Mbuti people. These groups branched off early in human history and have remained relatively genetically isolated since then. Haplogroups L1, L2 and L3 are descendents of L1-6 and are largely confined to Africa. The macro haplogroups M and N, which are the lineages of the rest of the world outside Africa, descend from L3.

Y-chromosomal DNA

The mutations defining macro-haplogroup CT (all Y haplogroups except A and B) predate the "Out of Africa" migration, its descendent macro-group DE being confined to Africa. The mutations that distinguish Haplogroup C from all other descendants of CR have occurred some 60,000 years ago, shortly after the first Out of Africa migration.

Haplogroup F originated some 45,000 years ago, either in North Africa (in which case it would point to a second wave of out-of-Africa migration) or in South Asia. More than

90% of males not native to Africa are descended in direct male line from the first bearer of haplogroup F.

Autosomal DNA

Analysis of 53 populations from genome-wide SNP data from 1138 unrelated individuals revealed that the population groups studied fell into just three genetic groups: Africans, Eurasians (which includes natives of Europe and the Middle East and Southwest Asians east to present-day Pakistan) and East Asians, which includes natives of Asia, Japan, Southeast Asia, the Americas and Oceania. The study determined that most ethnic group differences can be attributed to genetic drift, with modern African populations having greater genetic diversity than the other two genetic groups consistent with human origin in Africa.

Other analyses of autosomal DNA from modern humans, however, indicated a likelihood of recent admixture from archaic human populations from outside of Africa. In 2010, analysis of two sources of archaic human autosomal DNA provided evidence for specific instances of admixture, in the form of a 1-4% shared genome between neanderthals and nonafrican modern humans not shared by modern Africans and a 4-6% shared genome between an archaic human recently discovered in denisova and modern melanesians not shared by other modern humans.

Exodus from Africa

Red Sea crossing

Some 70 millennia ago, a part of the bearers of mitochondrial haplogroup L3 migrated from East Africa into the Near East.

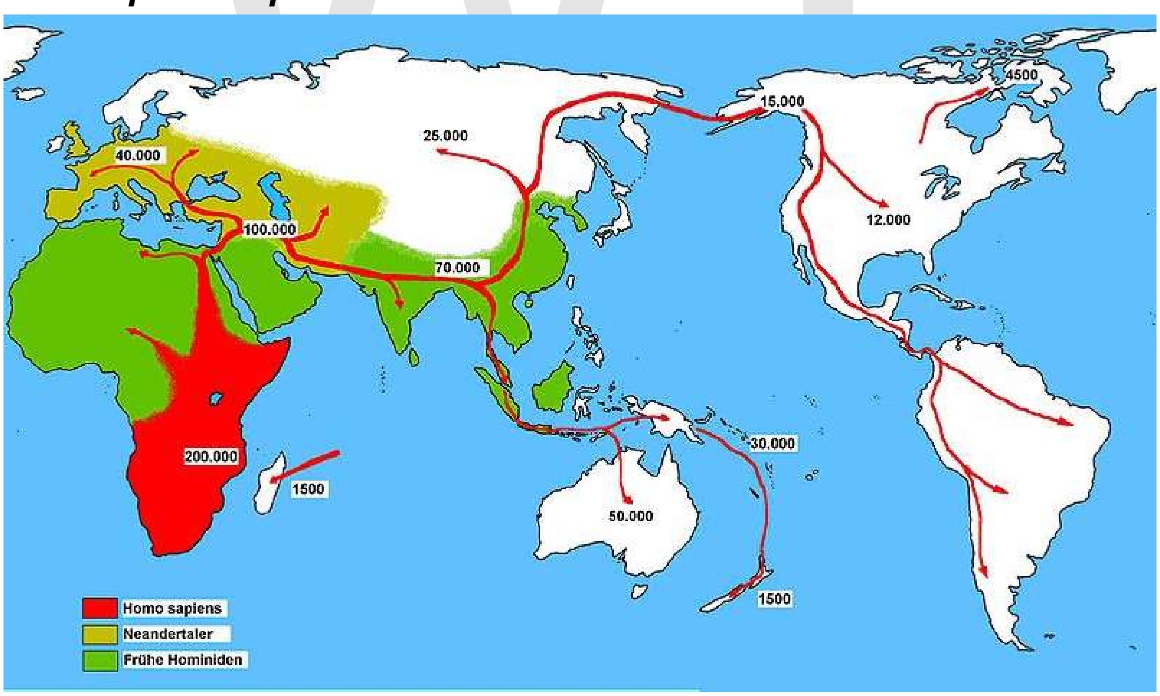
Some scientists believe that only a few people left Africa in a single migration that went on to populate the rest of the world, based in the fact that only descents of L3 are found outside Africa. From that settlement, some others point to the possibility of several waves of expansion. For example, Wells says that the early travelers followed the southern coastline of Asia, crossed about 250 kilometers [155 miles] of sea and colonized Australia by around 50,000 years ago. The Aborigines of Australia, Wells says, are the descendants of the first wave of migrations.

It has been estimated that from a population of 2,000 to 5,000 in Africa, only a small group of possibly 150 people crossed the Red Sea. This is because, of all the lineages present in Africa, only the daughters of one lineage, L3, are found outside Africa. Had there been several migrations one would expect more than one African lineage outside Africa. L3's daughters, the M and N lineages, are found in very low frequencies in Africa (although haplogroup M1 is very ancient and diversified in North and Northeast Africa) and appear to be recent arrivals. A possible explanation is that these mutations occurred in East Africa shortly before the exodus and by the founder effect became the dominant haplogroups after the exodus from Africa. Alternatively, the mutations may have arisen shortly after the exodus from Africa.

Other scientists have proposed a Multiple Dispersal Model, in which there were two migrations out of Africa, one across the Red Sea travelling along the coastal regions to India (the Coastal Route), which would be represented by Haplogroup M. Another group of migrants with Haplogroup N followed the Nile from East Africa, heading northwards and crossing into Asia through the Sinai. This group then branched in several directions, some moving into Europe and others heading east into Asia. This hypothesis attempts to explain why Haplogroup N is predominant in Europe and why Haplogroup M is absent in Europe. Evidence of the coastal migration is hypothesized to have been destroyed by the rise in sea levels during the Holocene epoch. Alternatively, a small European founder population that initially expressed both Haplogroup M and N could have lost Haplogroup M through random genetic drift resulting from a bottleneck (i.e. a founder effect).

Today at the Bab-el-Mandeb straits the Red Sea is about 12 miles (20 kilometres) wide, but 50,000 years ago it was much narrower and sea levels were 70 meters lower. Though the straits were never completely closed, there may have been islands in between which could be reached using simple rafts. Shell middens 125,000 years old have been found in Eritrea, indicating the diet of early humans included seafood obtained by beachcombing.

Subsequent expansion



Map of early human migrations

From the Near East, these populations spread east to South Asia by 50,000 years ago and on to Australia by 40,000 years ago, *Homo sapiens* for the first time colonizing territory never reached by *Homo erectus*. Europe was reached by Cro-Magnon some 40,000 years ago. East Asia (Korea, Japan) was reached by 30,000 years ago. It is disputed whether subsequent migration to North America took place around 30,000 years ago, or only considerably later, around 14,000 years ago.

The group that crossed the Red Sea travelled along the coastal route around the coast of Arabia and Persia until reaching India, which appears to be the first major settling point. M is found in high frequencies along the southern coastal regions of Pakistan and India and it has the greatest diversity in India, indicating that it is here where the mutation may have occurred. Sixty percent of the Indian population belong to Haplogroup M. The indigenous people of the Andaman Islands also belong to the M lineage. The Andamanese are thought to be offshoots of some of the earliest inhabitants in Asia because of their long isolation from mainland Asia. They are evidence of the coastal route of early settlers that extends from India along the coasts of Thailand and Indonesia all the way to Papua New Guinea. Since M is found in high frequencies in highlanders from New Guinea as well and both the Andamanese and New Guineans have dark skin and Afro-textured hair, some scientists believe they are all part of the same wave of migrants who departed across the Red Sea ~60,000 years ago in the Great Coastal Migration. Notably, the findings of Harding et al. (2000, p. 1355) show that, at least with regard to dark skin color, the haplotype background of Papua New Guineans at MC1R (one of a number of genes involved in melanin production) is identical to that of Africans (barring a single silent mutation). Thus, although these groups are distinct from Africans at other loci (due to drift, bottlenecks, etc), it is evident that selection for the dark skin color trait likely continued (at least at MC1R) following the exodus. This would support the hypothesis that suggests that the original migrants from Africa resembled pre-exodus Africans (at least in skin color) and that the present day remnants of this ancient phenotype can be seen among contemporary Africans andamanese and New Guineans. Others suggest that their physical resemblance to Africans could be the result of convergent evolution.

From Arabia to India the proportion of haplogroup M increases eastwards: in eastern India, M outnumbers N by a ratio of 3:1. However, crossing over into East Asia, Haplogroup N reappears as the dominant lineage. M is predominant in South East Asia but amongst Indigenous Australians N reemerges as the more common lineage. This discontinuous distribution of Haplogroup N from Europe to Australia can be explained by founder effects and population bottlenecks.

Competing hypotheses

The multiregional hypothesis, initially proposed by Milford Wolpoff, holds that the evolution of humans from *H. erectus* at the beginning of the Pleistocene 1.8 million years BP to the present day has been within a single, continuous worldwide population. Proponents of multiregional origin reject the assumption of an infertility barrier between ancient Eurasian and African populations of *Homo*. Multiregional proponents point to the fossil record and genetic evidence in chromosomal DNA. One study suggested that at least 5% of the human modern gene pool can be attributed to ancient admixture, which in Europe would be from the Neanderthals.

A recently discovered fossilized mandible that is putatively a hybrid between *Homo sapiens* and an earlier hominid, that is likely to be 110,000 years old, has been interpreted as a challenge to the recent out-of-Africa hypothesis. However, some scholars doubt that the fossil represents a Homo sapiens hybrid.

Chapter- 7

Human Genetic Variation

Human genetic variation is the genetic diversity of humans and represents the total amount of genetic characteristics observed within the human species. Genetic differences are observed between humans at both the individual and the population level. There may be multiple variants of any given gene in the human population (alleles), leading to polymorphism. Many genes are not polymorphic, meaning that only a single allele is present in the population: that allele is then said to be fixed.

No two humans are genetically identical. Even monozygotic twins, who develop from one zygote, have infrequent genetic differences due to mutations occurring during development and gene copy number variation has been observed. Differences between individuals, even closely related individuals, are the key to techniques such as genetic fingerprinting. Alleles occur at different frequencies in different human populations, with populations that are more geographically and ancestrally remote tending to differ more.

Causes of differences between individuals include the exchange of genes during meiosis and various mutational events. There are at least two reasons why genetic variation exists between populations. Natural selection may confer an adaptive advantage to individuals in a specific environment if an allele provides a competitive advantage. Alleles under selection are likely to occur only in those geographic regions where they confer an advantage. The second main cause of genetic variation is due to the high degree of neutrality of most mutations. Most mutations do not appear to have any selective effect one way or the other on the organism. The main cause is genetic drift, this is the effect of random changes in the gene pool. In humans, founder effect and past small population size (increasing the likelihood of genetic drift) may have had an important influence in neutral differences between populations.

The theory that humans recently migrated out of Africa is sometimes given as an example of this. It has been theorized that the population which migrated out of Africa only represented a small fraction of the genetic variation in Africa and that this is a contributing cause of the observed lower levels of diversity in all indigenous humans outside of Africa. Generally, more recent neutral polymorphisms caused by mutation are likely to be relatively geographically localized and rare, while older polymorphisms are more likely to be shared by a wider range of human groups. The large majority of observed genetic variation occurs within a population in any geographic region and not between populations in different regions, although it is still usually possible to accurately identify the geographic origins of any individual's ancestors by genetic means.

The study of human genetic variation has both evolutionary significance and medical applications. The study can help scientists understand ancient human population migrations as well as how different human groups are biologically related to one another. From a medical perspective the study of human genetic variation may be important because some disease causing alleles occur at a greater frequency in people from specific geographic regions.

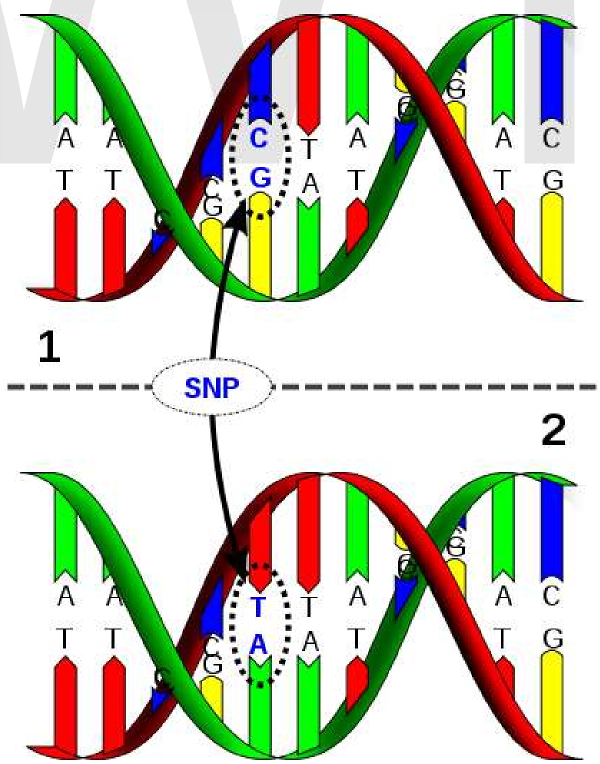
Genetic variation

Genetic variation, variation in alleles of genes, occurs both within and among populations. Genetic variation is important because it provides the "raw material" for natural selection.

Measures of variation

"Genetic variation among individual humans occurs on many different scales, ranging from gross alterations in the human karyotype to single nucleotide changes."

Single nucleotide polymorphisms



DNA molecule 1 differs from DNA molecule 2 at a single base-pair location (a C/T polymorphism).

Nucleotide diversity is based on single mutations called single nucleotide polymorphisms (SNPs). The nucleotide diversity between humans is about 0.1%, which is 1 difference per 1,000 base pairs. A difference of 1 in 1,000 nucleotides between two humans chosen at random amounts to approximately 3 million nucleotide differences since the human genome has about 3 billion nucleotides. Most of these SNPs are neutral but some are functional and influence phenotypic differences between humans through alleles. It is estimated that a total of 10 million SNPs exist in the human population of which at least 1% are functional.

Copy number variation

More recently a better understanding of the structure of the genome has been gained with the publication of two examples of full sequences of an individual's genome. This represents a new development because the Human Genome Project and a parallel project by Celera Genomics produced two haploid sequences, both of which were an amalgamation of sequences from many individuals. Recently the diploid sequences of both Craig Venter and James Watson have been published. Analysis of diploid sequences has shown that non-SNP variation accounts for much more human genetic variation than single nucleotide diversity. This non-SNP variation includes copy number variation and results from deletions, inversions, insertions and duplications. It is estimated that approximately 0.4% of the genomes of unrelated people typically differ with respect to copy number. When copy number variation is included, human to human genetic variation is estimated to be at least 0.5% (99.5% similarity). Copy number variations are inherited but can also arise during development.

Epigenetics

Epigenetics is another type of genetic variation. "This type of variation arises from chemical tags that attach to DNA and affect how it gets read. The chemical tags, called epigenetic markings, act as switches that control how genes can be read." At some alleles, the epigenetic state of the DNA and associated phenotype, can be inherited transgenerationally.

Genetic variability

Genetic variability is a measure of the tendency of individual genotypes in a population to vary (become different) from one another. Variability is different from genetic diversity, which is the amount of variation seen in a particular population. The variability of a trait describes how much that trait tends to vary in response to environmental and genetic influences.

Clines

In biology, a cline is a term used to describe a continuum of species, populations, races, varieties, or forms of organisms that exhibit gradual phenotypic and/or genetic differences over a geographical area, typically as a result of environmental heterogeneity.

In the scientific study of human genetic variation, a gene cline can be rigorously defined and subjected to quantitative metrics.

Haplogroups

In the study of molecular evolution, a haplogroup is a group of similar haplotypes that share a common ancestor with a single nucleotide polymorphism (SNP) mutation. Haplogroups pertain to deep ancestral origins dating back thousands of years.

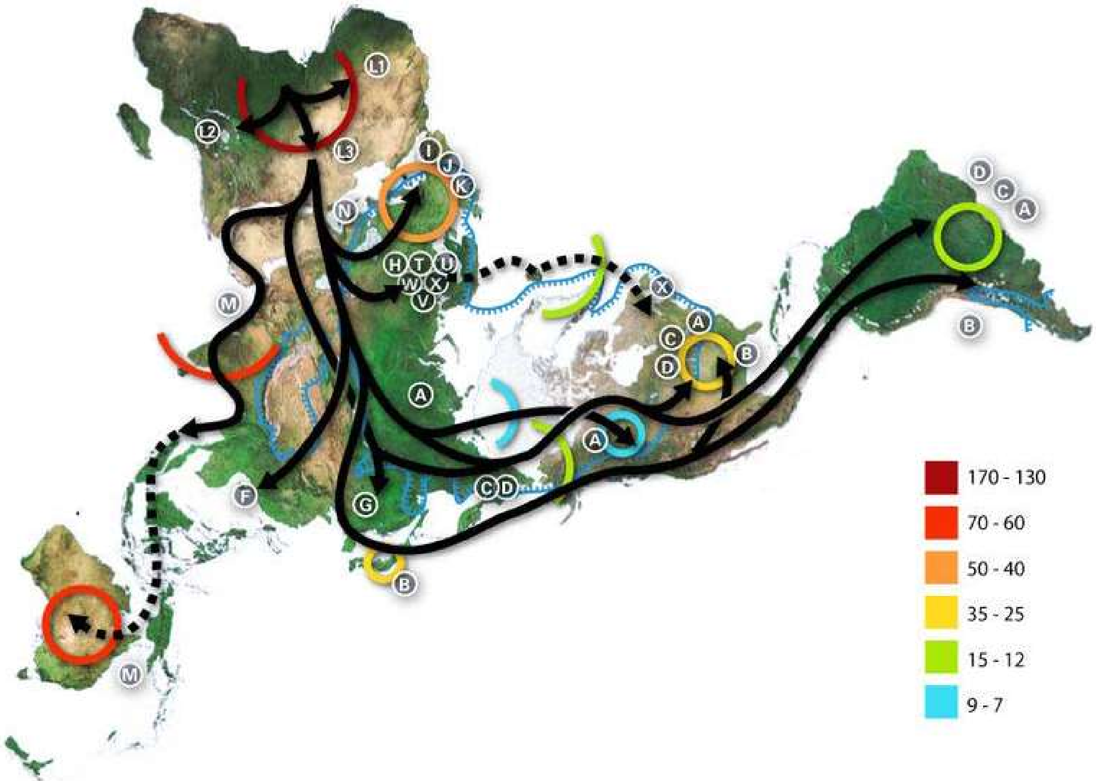
In human genetics, the haplogroups most commonly studied are Y-chromosome (Y-DNA) haplogroups and mitochondrial DNA (mtDNA) haplogroups, both of which can be used to define genetic populations. Y-DNA is passed solely along the patrilineal line, from father to son, while mtDNA is passed down the matrilineal line, from mother to both daughter and son. The Y-DNA and mtDNA may change by chance mutation at each generation.

Variable number tandem repeats

A variable number tandem repeat (VNTR) is a location in a genome where a short nucleotide sequence is organized as a tandem repeat. These can be found on many chromosomes and often show variations in length between individuals. Each variant acts as an inherited allele, allowing them to be used for personal or parental identification. Their analysis is useful in genetics and biology research, forensics and DNA fingerprinting.

There are two principal families of VNTRs: microsatellites and minisatellites. The former are repeats of sequences less than about 5 base pairs in length, while the latter involve longer blocks.

History and geographic distribution



Map of the migration of modern humans out of Africa, based on mitochondrial DNA. Colored rings indicate thousand years before present.

A 10-year study published in April 2009 analyzed the patterns of variation at 1,327 DNA markers of 121 African populations, 4 African American populations and 60 non-African populations. The research showed that there is more human genetic diversity in Africa than anywhere else on Earth. The genetic structure of Africans was traced to 14 ancestral population clusters and the ancestral origin of humans was determined to probably be located in southern Africa, near the border of Namibia and South Africa.

Human genetic diversity decreases in native populations with migratory distance from Africa and this is thought to be the result of bottlenecks during human migration, which are events that temporarily reduce population size. It has been shown that variations in skull measurements decrease with distance from Africa at the same rate as the decrease in genetic diversity. These data support the Out of Africa theory over the multiregional origin of modern humans hypothesis. The aforementioned April 2009 study identifies the likely origin of modern human migration as being in southwestern Africa, near the coastal border of Namibia and Angola and the exit point out of Africa as being in East Africa.

The *recent African origin of modern humans* is the mainstream model describing the origin and early dispersal of anatomically modern humans, *Homo sapiens sapiens*. The theory is known popularly as the *(Recent) Out-of-Africa* model. The hypothesis originated in the 19th century, with Darwin's *Descent of Man*, but remained speculative until the 1980s when it was corroborated based on a study of present-day mitochondrial DNA, combined with evidence based on physical anthropology of archaic specimens.

According to both genetic and fossil evidence, archaic Homo sapiens evolved to anatomically modern humans solely in Africa, between 200,000 and 100,000 years ago, with members of one branch leaving Africa by 60,000 years ago and over time replacing earlier human populations such as Neanderthals and *Homo erectus*. According to this theory, around the above time frame, one of the African subpopulations went through a process of speciation prohibiting gene flow between African and Eurasian Human populations.

Population genetics

In the field of population genetics, it is believed that the distribution of neutral polymorphisms among contemporary humans reflects human demographic history. It is believed that humans passed through a population bottleneck before a rapid expansion coinciding with migrations out of Africa leading to an African-Eurasian divergence around 100,000 years ago (ca. 5,000 generations), followed by a European-Asian divergence about 40,000 years ago (ca. 2,000 generations). Richard G. Klein, Nicholas Wade and Spencer Wells, among others, have postulated that modern humans did not leave Africa and successfully colonize the rest of the world until as recently as 60,000 - 50,000 years B.P., pushing back the dates for subsequent population splits as well.

The rapid expansion of a previously small population has two important effects on the distribution of genetic variation. First, the so-called founder effect occurs when founder populations bring only a subset of the genetic variation from their ancestral population. Second, as founders become more geographically separated, the probability that two individuals from different founder populations will mate becomes smaller. The effect of this assortative mating is to reduce gene flow between geographical groups and to increase the genetic distance between groups. The expansion of humans from Africa affected the distribution of genetic variation in two other ways. First, smaller (founder) populations experience greater genetic drift because of increased fluctuations in neutral polymorphisms. Second, new polymorphisms that arose in one group were less likely to be transmitted to other groups as gene flow was restricted.

Our history as a species also has left genetic signals in regional populations. For example, in addition to having higher levels of genetic diversity, populations in Africa tend to have lower amounts of linkage disequilibrium than do populations outside Africa, partly because of the larger size of human populations in Africa over the course of human history and partly because the number of modern humans who left Africa to colonize the rest of the world appears to have been relatively low (Gabriel *et al.* 2002). In contrast, populations that have undergone dramatic size reductions or rapid expansions in the past and populations formed by the mixture of previously separate ancestral groups can have unusually high levels of linkage disequilibrium (Nordborg and Tavare 2002).

Many other geographic, climatic and historical factors have contributed to the patterns of human genetic variation seen in the world today. For example, population processes associated with colonization, periods of geographic isolation, socially reinforced endogamy and natural selection all have affected allele frequencies in certain populations (Jorde *et al.* 2000b; Bamshad and Wooding 2003). In general, however, the recency of our common ancestry and continual gene flow among human groups have limited genetic differentiation in our species.

Distribution of variation

The distribution of genetic variants within and among human populations are impossible to describe succinctly because of the difficulty of defining a "population," the clinal nature of variation and heterogeneity across the genome (Long and Kittles 2003). In general, however, an average of 85% of genetic variation exists within local populations, ~7% is between local populations within the same continent and ~8% of variation occurs between large groups living on different continents,. (Lewontin 1972; Jorde *et al.* 2000a; Hinds *et al.* 2005). The recent African origin theory for humans would predict that in Africa there exists a great deal more diversity than elsewhere and that diversity should decrease the further from Africa a population is sampled. Long and Kittles show that indeed, African populations contain about 100% of human genetic diversity, whereas in populations outside of Africa diversity is much reduced, for example in their population from New Guinea only about 70% of human variation is captured.

Phenotypic variation

Sub-Saharan Africa has the most human genetic diversity and the same has been shown to hold true for phenotypic diversity. Genetic diversity decreases smoothly with migratory distance from that region, which many scientists believe to be the origin of modern humans and that decrease is mirrored by a decrease in phenotypic variation. Skull measurements are an example of a physical attribute whose within-population variation decreases with distance from Africa.

The distribution of many physical traits resembles the distribution of genetic variation within and between human populations (American Association of Physical Anthropologists 1996; Keita and Kittles 1997). For example, ~90% of the variation in human head shapes occurs within continental groups and ~10% separates groups, with a greater variability of head shape among individuals with recent African ancestors (Relethford 2002).

A prominent exception to the common distribution of physical characteristics within and among groups is skin color. Approximately 10% of the variance in skin color occurs within groups and ~90% occurs between groups (Relethford 2002). This distribution of skin color and its geographic patterning — with people whose ancestors lived predominantly near the equator having darker skin than those with ancestors who lived predominantly in higher latitudes — indicate that this attribute has been under strong selective pressure. Darker skin appears to be strongly selected for in equatorial regions to prevent sunburn, skin cancer, the photolysis of folate and damage to sweat glands (Sturm *et al.* 2001; Rees 2003).

Neanderthal admixture

Interbreeding of Neanderthals and anatomically modern humans during the Middle Paleolithic is a hypothesis. In May 2010, the Neanderthal Genome Project presented genetic evidence that interbreeding did likely take place and that a small but significant portion of Neanderthal admixture is present in the DNA of modern non-African populations.

Categorization of the world population

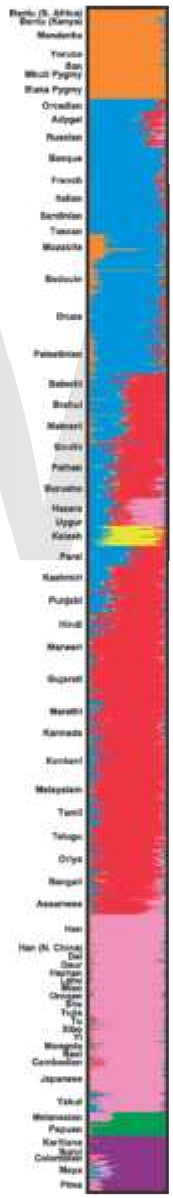


Chart showing human genetic clustering

New data on human genetic variation has reignited the debate surrounding race. Most of the controversy surrounds the question of how to interpret this new data and whether conclusions based on existing data are sound. A large majority of researchers endorse the view that continental groups do not constitute different subspecies. However, other researchers still debate whether evolutionary lineages should rightly be called "races". These questions are particularly pressing for ancestry related health issues, where self-identified race is often used as an indicator of ancestry.

Although the genetic differences among human groups are relatively small, these differences in certain genes such as duffy, ABCC11, SLC24A5, called ancestry-informative markers (AIMs) nevertheless can be used to reliably situate many individuals within broad, geographically based groupings or self-identified race. For example, computer analyses of hundreds of polymorphic loci sampled in globally distributed populations have revealed the existence of genetic clustering that roughly is associated with groups that historically have occupied large continental and subcontinental regions (Rosenberg *et al.* 2002; Bamshad *et al.* 2003).

Some commentators have argued that these patterns of variation provide a biological justification for the use of traditional racial categories. They argue that the continental clusterings correspond roughly with the division of human beings into sub-Saharan Africans; Europeans, Western Asians, Central Asians, Southern Asians and Northern Africans; Eastern Asians, Southeast Asians, Polynesians and Native Americans; and other inhabitants of Oceania (Melanesians, Micronesians & Australian Aborigines) (Risch *et al.* 2002). Other observers disagree, saying that the same data undercut traditional notions of racial groups (King and Motulsky 2002; Calafell 2003; Tishkoff and Kidd 2004). They point out, for example, that major populations considered races or subgroups within races do not necessarily form their own clusters.

Furthermore, because human genetic variation is clinal, many individuals affiliate with two or more continental groups. Thus, the genetically based "biogeographical ancestry" assigned to any given person generally will be broadly distributed and will be accompanied by sizable uncertainties (Pfaff *et al.* 2004).

In many parts of the world, groups have mixed in such a way that many individuals have relatively recent ancestors from widely separated regions. Although genetic analyses of large numbers of loci can produce estimates of the percentage of a person's ancestors coming from various continental populations (Shriver *et al.* 2003; Bamshad *et al.* 2004), these estimates may assume a false distinctiveness of the parental populations, since human groups have exchanged mates from local to continental scales throughout history (Cavalli-Sforza *et al.* 1994; Hoerder 2002). Even with large numbers of markers, information for estimating admixture proportions of individuals or groups is limited and estimates typically will have wide confidence intervals (Pfaff *et al.* 2004).

Lewontin's Fallacy

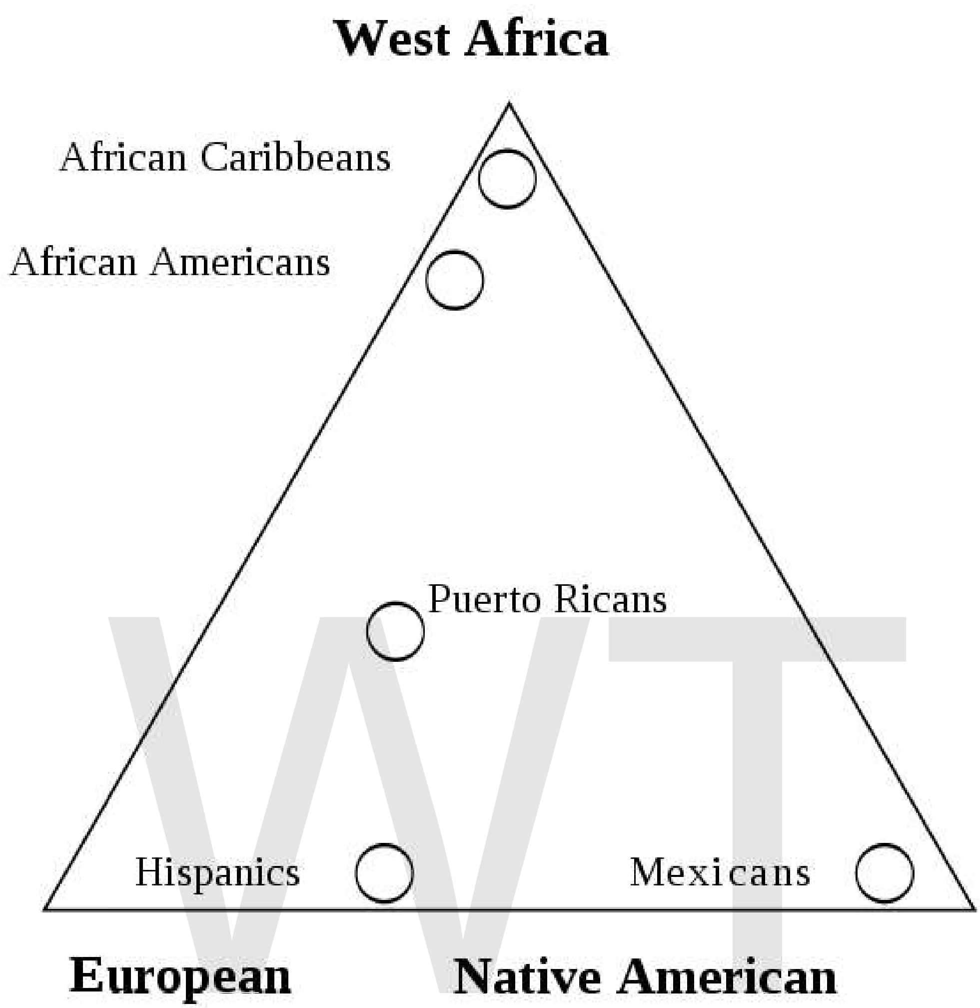
In 2003 A. W. F. Edwards wrote a paper called Lewontin's Fallacy, rebutting the argument that because most genetic variation is within-group, classification of humans is not possible. He claimed that this conclusion ignores the fact that most of the information that distinguishes populations is hidden in the correlation structure of the data and not simply in the variation of the individual factors. Edwards concludes that "It is not true that 'racial classification is ... of virtually no genetic or taxonomic significance' or that 'you can't predict someone's race by their genes'." Undeterred, in an article titled "Confusions About Human Races" published in 2006, Lewontin maintains that race is no more than a social construct.

Genetic clustering

Genetic data can be used to infer population structure and assign individuals to groups that often correspond with their self-identified geographical ancestry. Recently, Lynn Jorde and Steven Wooding argued that "Analysis of many loci now yields reasonably accurate estimates of genetic similarity among individuals, rather than populations. Clustering of individuals is correlated with geographic origin or ancestry."

Forensic anthropology

Forensic anthropologists can determine race (e.g. Asian, African, or European ancestry) from skeletal remains with a high degree of accuracy by conducting bone analysis. Studies have shown that individual test methods such as midfacial measurements and femur traits can be over 80 percent accurate and in combination can achieve very high levels of accuracy. The skeletons of mixed-race individuals can, however, exhibit characteristics of more than one racial group. Despite the success of this method with the remains of individuals with ancestry predominantly from a single race, anthropologists, including George W. Gill and C. Loring Brace, disagree on whether race is a valid biological concept.



Triangle plot shows average admixture of five North American ethnic groups. Individuals that self-identify with each group can be found at many locations on the map, but on average groups tend to cluster differently.

Admixture

Miscegenation between two populations reduces the average genetic distance between the populations. During the Age of Discovery which began in the early 15th century, European explorers sailed all around the globe, reaching all the major continents. In the process they came into contact with many populations that had been isolated for thousands of years. It is generally accepted that the Tasmanian aboriginals were the most isolated group on the planet. They were driven to extinction by European explorers, however a number of their descendants survive today as a result of admixture with Europeans. This is an example of how modern migrations have begun to reduce the genetic divergence of the human race.

The demographic composition of the old world has not changed significantly since the age of discovery. However new world demographics were radically changed within a short time following the voyage of Columbus. The colonization of the Americas brought Native Americans into contact with the distant populations of Europe, Africa and Asia. As a result many countries in the Americas have significant and complex multiracial populations. Furthermore many who identify themselves by only one race still have multiracial ancestry.

Health

Differences in allele frequencies contribute to group differences in the incidence of some monogenic diseases and they may contribute to differences in the incidence of some common diseases (Risch *et al.* 2002; Burchard *et al.* 2003; Tate and Goldstein 2004). For the monogenic diseases, the frequency of causative alleles usually correlates best with ancestry, whether familial (for example, Ellis-van Creveld syndrome among the Pennsylvania Amish), ethnic (Tay-Sachs disease among Ashkenazi Jewish populations), or geographical (hemoglobinopathies among people with ancestors who lived in malarial regions). To the extent that ancestry corresponds with racial or ethnic groups or subgroups, the incidence of monogenic diseases can differ between groups categorized by race or ethnicity and health-care professionals typically take these patterns into account in making diagnoses.

Even with common diseases involving numerous genetic variants and environmental factors, investigators point to evidence suggesting the involvement of differentially distributed alleles with small to moderate effects. Frequently cited examples include hypertension (Douglas *et al.* 1996), diabetes (Gower *et al.* 2003), obesity (Fernandez *et al.* 2003) and prostate cancer (Platz *et al.* 2000). However, in none of these cases has allelic variation in a susceptibility gene been shown to account for a significant fraction of the difference in disease prevalence among groups and the role of genetic factors in generating these differences remains uncertain (Mountain and Risch 2004).

Neil Risch of Stanford University has proposed that self-identified race/ethnic group could be a valid means of categorization in the USA for public health and policy considerations. While a 2002 paper by Noah Rosenberg's group makes a similar claim "The structure of human populations is relevant in various epidemiological contexts. As a result of variation in frequencies of both genetic and nongenetic risk factors, rates of disease and of such phenotypes as adverse drug response vary across populations. Further, information about a patient’s population of origin might provide health care practitioners with information about risk when direct causes of disease are unknown."

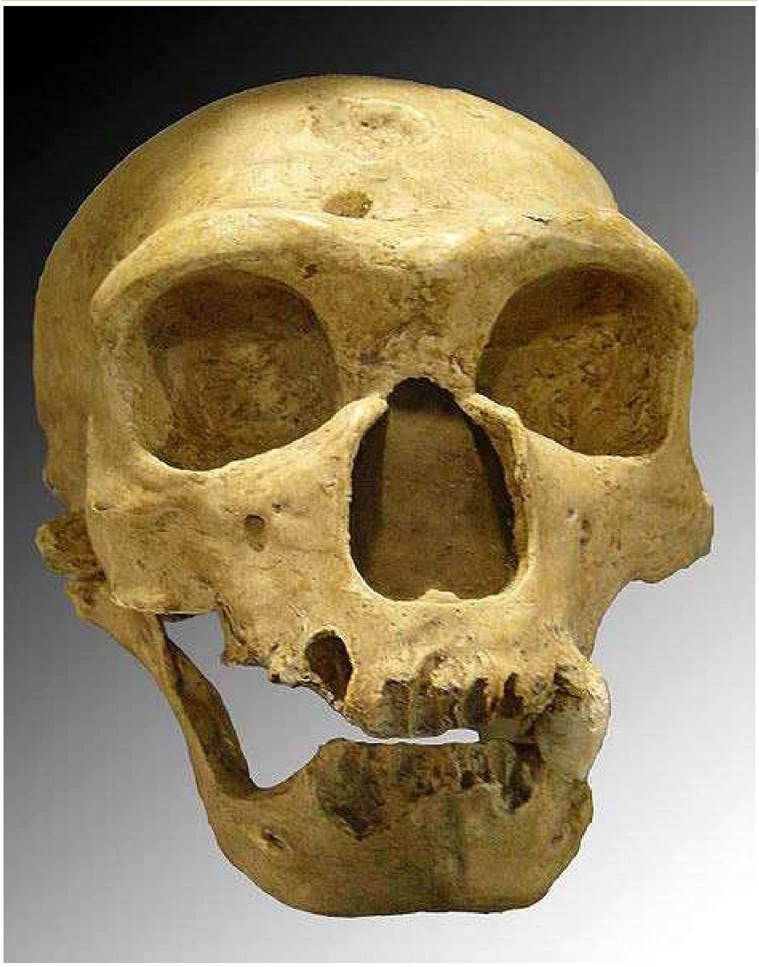
Genome projects

Human genome projects are scientific endeavors that determine or study the structure of the human genome. The Human Genome Project was a landmark genome project.

Chapter- 8

Neanderthal

Neanderthal Fossil range: Middle to Late Pleistocene0.6–0.03 Ma

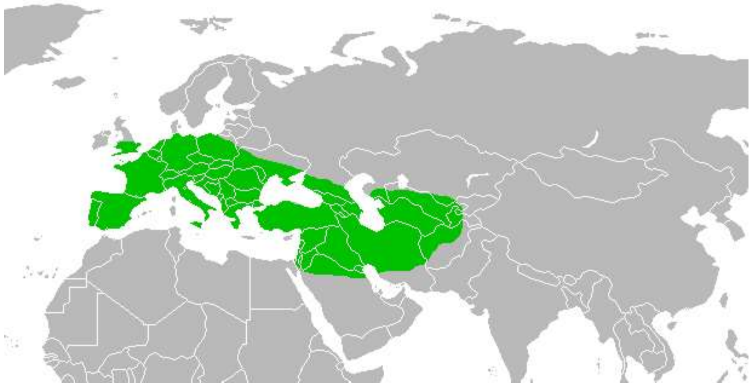


A Skull, La Chapelle-aux-Saints

Mounted Neanderthal skeleton, American Museum of Natural History

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Primates
Family:	Hominidae
Genus:	*Homo*
Species:	***H. neanderthalensis***
Binomial name	
Homo neanderthalensis	

King, 1864



Range of *Homo neanderthalensis*. Eastern and northern ranges may be extended to include Okladnikov in Altai and Mamotnaia in Ural

Synonyms

Palaeoanthropus neanderthalensis
H. s. neanderthalensis

The **Neanderthal** (short for **Neanderthal Man**; in modern orthography **Neandertal**) is an extinct member of the *Homo* genus that is known from Pleistocene specimens found in Europe and parts of western and central Asia. Neanderthals are either classified as a subspecies (or race) of modern humans (***Homo sapiens neanderthalensis***) or as a separate human species (***Homo neanderthalensis***).

The first proto-Neanderthal traits appeared in Europe as early as 600,000–350,000 years ago. Proto-Neanderthal traits are occasionally grouped to another phenetic 'species', *Homo heidelbergensis*, or a migrant form, *Homo rhodesiensis*.

By 130,000 years ago, complete Neanderthal characteristics had appeared. These characteristics then disappeared in Asia by 50,000 years ago and in Europe by about 30,000 years ago, with no further individuals having enough Neanderthal morphological traits to be considered as part of *Homo neanderthalensis*.

Current (as of 2010) genetic evidence suggests interbreeding took place with *Homo sapiens* (anatomically modern humans) between roughly 80,000 and 50,000 years ago in the Middle East, resulting in 1–4% of the genome of people from Eurasia having been contributed by Neanderthals.

The youngest Neanderthal finds include Hyaena Den (UK), considered older than 30,000 years ago, while the Vindija (Croatia) Neanderthals have been re-dated to between 32,000 and 33,000 years ago. No definite specimens younger than 30,000 years ago have been found; however, evidence of fire by Neanderthals at Gibraltar indicate they may have survived there until 24,000 years ago. Cro-Magnon or early modern human skeletal remains with 'Neanderthal traits' were found in Lagar Velho (Portugal), dated to 24,500 years ago and controversially interpreted as indications of extensively admixed populations.

Neanderthal stone tools provide further evidence for their presence where skeletal remains have not been found. The last traces of Mousterian culture, a type of stone tools associated with Neanderthals, were found in Gorham's Cave on the remote south-facing coast of Gibraltar. Other tool cultures sometimes associated with Neanderthal include Châtelperronian, Aurignacian and Gravettian, with the latter extending to 22,000 years ago, the last indication of Neanderthal presence.

Neanderthal cranial capacity is thought to have been as large as that of *Homo sapiens*, perhaps larger, indicating their brain size may have been comparable, as well. In 2008, a group of scientists created a study using three-dimensional computer-assisted reconstructions of Neanderthal infants based on fossils found in Russia and Syria, showing that they had brains as large as modern humans' at birth and larger than modern humans' as adults. On average, the height of Neanderthals was comparable to contemporaneous *Homo sapiens*. Neanderthal males stood about 165–168 cm (65–66 in) and were heavily built with robust bone structure. They were much stronger than *Homo sapiens*, having particularly strong arms and hands. Females stood about 152–156 cm (60–61 in).

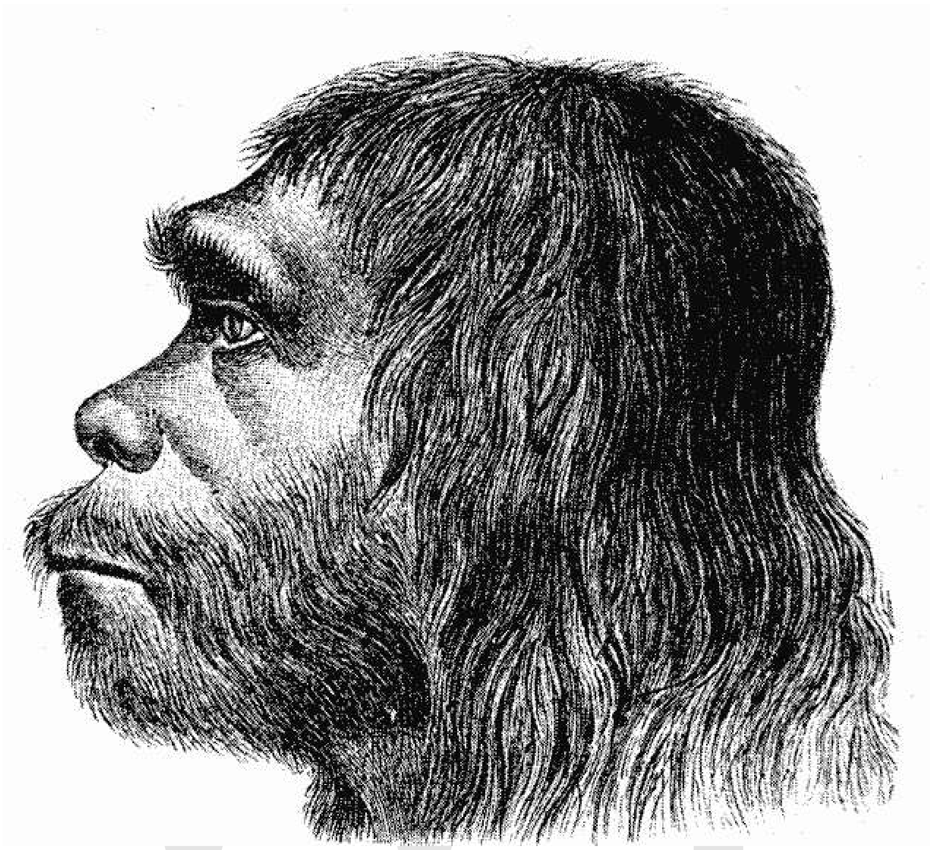
In 2010 a U.S. researcher reported finding cooked plant matter in the teeth of a Neanderthal skull, indicating the earlier belief they were exclusively (or almost exclusively) carnivorous and apex predators was incorrect.

Etymology

The Neanderthal is named after the Neandertal valley, formerly spelled *Neanderthal*, which is located about 12 km (7.5 mi) east of Düsseldorf, Germany. The valley itself was named after the theologian Joachim Neander, who lived nearby in Düsseldorf in the late 17th century. "Neander" is a classicized form of the common German surname Neumann. "Tal" (spelled "Thal" until the German spelling reform of 1901) is the German word for valley. The fossil discovered in the Neandertal in 1856, Neanderthal 1, was known as the "Neanderthal skull" or "Neanderthal cranium" in anthropological literature and the individual reconstructed on the basis of the skull was occasionally called the "Neanderthal man". The binomial name *Homo neanderthalensis*, extending the name "Neanderthal man" from the individual type specimen to the entire species, is due to the Anglo-Irish geologist William King (1864). The practice of referring to the members of the species simply as "the Neanderthals", singular "a Neanderthal", emerges in popular literature of the 1920s.

The spelling of the German word *Thal* ("dale, valley"), was changed to *Tal* in 1901 and the spelling of the valley was also changed accordingly to *Neandertal*. The former spelling is, however, often retained in English for the hominid. The spelling with *th* is in addition always used in scientific names throughout the world. In German, however, the modern spelling with *t* is used in referring to both the hominid and the valley. *Neandertal* is a widespread alternative spelling in English, becoming so common it is sometimes now listed first in dictionaries, for example MSN Encarta.

Classification



First reconstruction of a Neanderthal male

For some time, scientists have debated whether Neanderthals should be classified as *Homo neanderthalensis* or "*Homo sapiens neanderthalensis*", the latter placing Neanderthals as a subspecies of *Homo sapiens*. Some morphological studies support that *Homo neanderthalensis* is a separate species and not a subspecies. Others, for example University of Cambridge Professor Paul Mellars, say "no evidence has been found of cultural interaction" and evidence from mitochondrial DNA studies have been interpreted as evidence Neanderthals were not a subspecies of *H. sapiens*, though more recent genomic evidence showed otherwise.

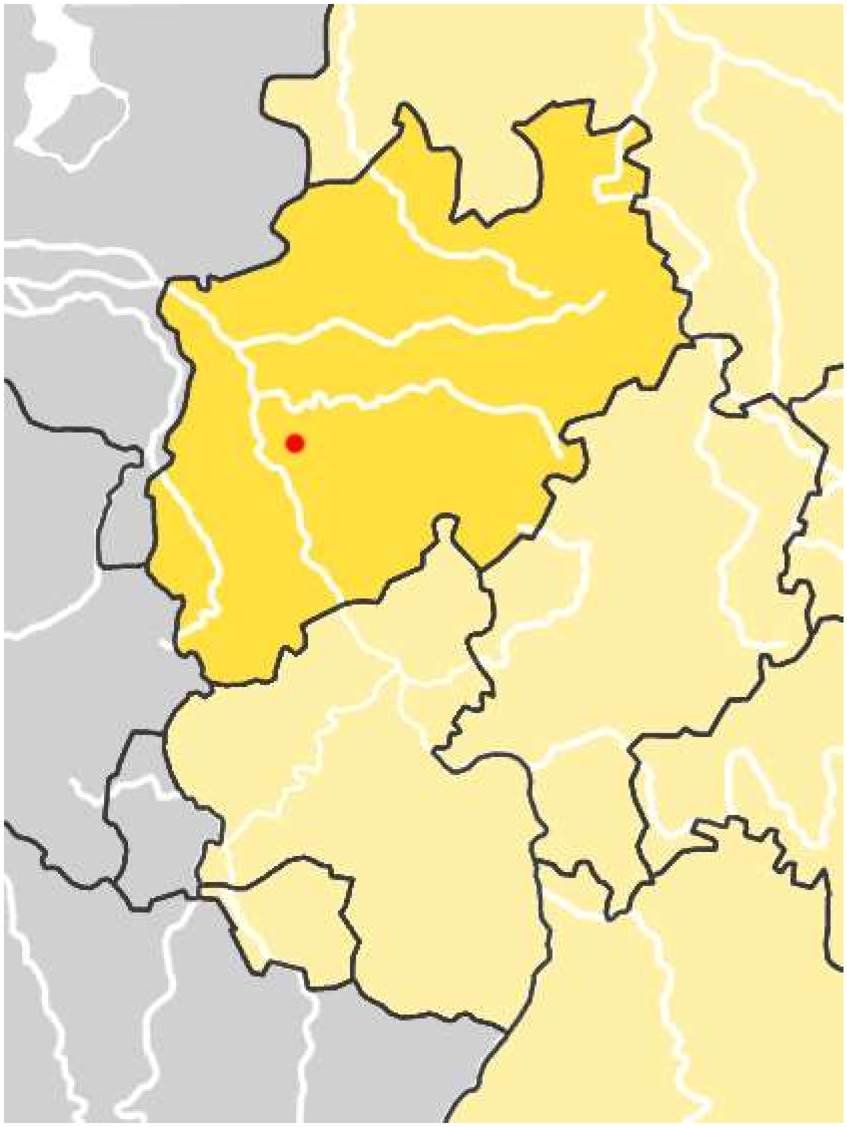
Neanderthals evolved from early *Homo* along a path similar to *Homo sapiens*, both deriving from a chimp-like ancestor between five and 10 million years ago. Like *H. sapiens*, Neanderthals are related to *Australopithecus*, *Homo habilis* and *Homo ergaster*; the exact descent remains uncertain. The last common ancestor between anatomically modern *Homo sapiens* and Neanderthals appears to be *Homo rhodesiensis*, named after an archaic *Homo sapiens* fossil, Broken hill 1 (Kabwe 1) discovered in the territory of Rhodesia in 1921.

Homo rhodesiensis arose in Africa an estimated 0.7 to 1 million years ago. The earliest estimates for *Homo rhodesiensis* reaching Europe are approximately 800 thousand years ago when a type of human referred to as *Homo antecessor* or *Homo cepranensis* already inhabited the region. These two human types may be forerunners to European *Homo heidelbergensis*; however, stone tools dating from 1.2 to 1.56 million years ago of an unknown creator have been discovered in south-western Europe. The evidence at the Sima de los Huesos (in the Atapuerca cave system on the Iberian Peninsula) suggests *Homo heidelbergensis* was already in Europe by 600,000 years ago.

Molecular phylogenetic analysis suggests *Homo rhodesiensis* and *Homo heidelbergensis* continued to intermix until 350,000 years ago, after which they were separate species and sometime within the last 200,000 years *Homo heidelbergensis* evolved into *Homo neanderthalensis*, the classic Neanderthal human. It appears the original Neanderthal population was, in fact, more distantly related to today's human than is *Homo heidelbergensis*. However, recent evidence of successful interbreeding between Neanderthals and modern humans has made that issue moot, at least insofar as some Neanderthal populations were concerned.

Discovery

The site of Kleine Feldhofer Grotte where the first Neanderthal was unearthed by miners in the 19th century



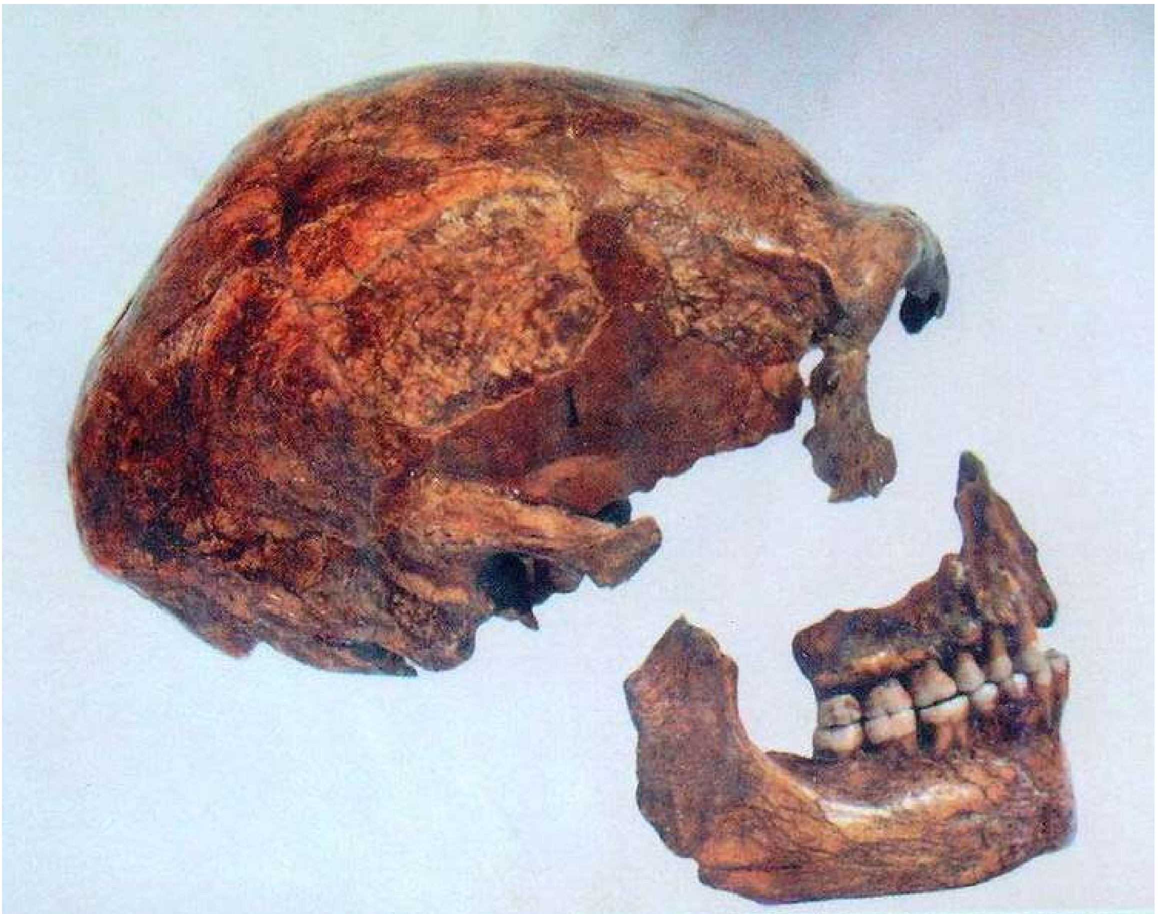
Location of Neander Valley, Germany. (The highlighted area is the modern federal state of North Rhine-Westphalia.)

Neanderthal skulls were first discovered in Engis, Belgium (1829) by Philippe-Charles Schmerling and in Forbes' Quarry, Gibraltar (1848), both prior to the type specimen discovery in a limestone quarry of the Neander Valley in Erkrath near Düsseldorf in August 1856, three years before Charles Darwin's *On the Origin of Species* was published.

The type specimen, dubbed Neanderthal 1, consisted of a skull cap, two femora, three bones from the right arm, two from the left arm, part of the left ilium, fragments of a scapula and ribs. The workers who recovered this material originally thought it to be the remains of a bear. They gave the material to amateur naturalist Johann Carl Fuhlrott, who turned the fossils over to anatomist Hermann Schaaffhausen. The discovery was jointly announced in 1857.

The original Neanderthal discovery is now considered the beginning of paleoanthropology. These and other discoveries led to the idea these remains were from ancient Europeans who had played an important role in modern human origins. The bones of over 400 Neanderthals have been found since.

Timeline



Skull, found in 1886 in Spy, Belgium

Frontal bone of a neanderthal child from the cave of La Garigüela

Skull from La Chapelle aux Saints

- 1829: Neanderthal skulls were discovered in Engis, Belgium.
- 1848: Neanderthal skull found in Forbes' Quarry, Gibraltar. Called "an ancient human" at the time.
- 1856: Johann Karl Fuhlrott first recognized the fossil called "Neanderthal man", discovered in Neanderthal, a valley near Mettmann in what is now North Rhine-Westphalia, Germany.
- 1880: The mandible of a Neanderthal child was found in a secure context and associated with cultural debris, including hearths, Mousterian tools and bones of extinct animals.
- 1886: Two nearly perfect skeletons of a man and woman were found at Spy, Belgium at the depth of 16 ft with numerous Mousterian-type implements.
- 1899: Hundreds of Neanderthal bones were described in stratigraphic position in association with cultural remains and extinct animal bones.
- 1908: A nearly complete Neanderthal skeleton was discovered in association with Mousterian tools and bones of extinct animals.
- 1925: Francis Turville-Petre finds the 'Galilee Man' or 'Galilee Skull' in the Zuttiyeh Cave in Wadi Amud in Palestine (now Israel).
- 1953–1957: Ralph Solecki uncovered nine Neanderthal skeletons in Shanidar Cave in northern Iraq.
- 1975: Erik Trinkaus's study of Neanderthal feet confirmed they walked like modern humans.
- 1987: Thermoluminescence results from Israeli fossils date Neanderthals at Kebara to 60,000 BP and humans at Qafzeh to 90,000 BP. These dates were confirmed by electron spin resonance (ESR) dates for Qafzeh (90,000 BP) and Es Skhul (80,000 BP).
- 1991: ESR dates showed the Tabun Neanderthal was contemporaneous with modern humans from Skhul and Qafzeh.
- 1997: Matthias Krings *et al.* are the first to amplify Neanderthal mitochondrial DNA (mtDNA) using a specimen from Feldhofer grotto in the Neander valley.
- 2000: Igor Ovchinnikov, Kirsten Liden, William Goodman *et al.* retrieved DNA from a Late Neanderthal (29,000 BP) infant from Mezmaikaya Cave in the Caucasus.
- 2005: The Max Planck Institute for Evolutionary Anthropology launched a project to reconstruct the Neanderthal genome.
- 2006: The Max Planck Institute for Evolutionary Anthropology announced it planned to work with Connecticut-based 454 Life Sciences to reconstruct the Neanderthal genome.
- 2009: The Max Planck Institute for Evolutionary Anthropology announced the "first draft" of a complete Neanderthal genome is completed.
- 2010: Comparison of Neanderthal genome with modern humans from Africa and Eurasia shows 1–4% of modern non-African human genetic material is identical with Neanderthal DNA.
- 2010: Discovery of Neanderthal tools far away from the influence of homo sapiens indicate that the species might have been able to create and evolve tools on its own and therefore be more intelligent than previously thought. Furthermore, it was proposed that the Neanderthals might be more closely related

to homo sapiens that previously thought and that may in fact be a sub species of it.

Habitat and range

Sites where typical Neanderthal fossils have been found

Early Neanderthals lived in the Last Glacial age for a span of about 100,000 years. Because of the damaging effects the glacial period had on the Neanderthal sites, not much is known about the early species. Countries where their remains are known include most of Europe south of the line of glaciation, roughly along the 50th parallel north, including most of Western Europe, including the south coast of Great Britain, Central Europe and the Balkans, some sites in the Ukraine and in western Russia and outside of Europe in the Zagros Mountains and in the Levant.

Neanderthal fossils have not been found to date in Africa, but there have been finds rather close to Africa, both at Gibraltar and in the Levant. At some Levantine sites, Neanderthal remains, in fact, date after the same sites were vacated by *Homo sapiens*. Mammal fossils of the same time period show cold-adapted animals were present alongside these Neanderthals in this region of the Eastern Mediterranean. This implies Neanderthals were better adapted biologically to cold weather than *H. sapiens* and at times displaced *H. sapiens* in parts of the Middle East when the climate got cold enough. *Homo sapiens* appears to have been the only human type in the Nile River Valley during these periods and Neanderthals are not known to have ever lived south-west of modern Israel. When further climate change caused warmer temperatures, the Neanderthal range likewise retreated to the north along with the cold-adapted species of mammals. Apparently these weather-induced population shifts took place before "modern" people secured competitive advantages over the Neanderthal, as these shifts in range took place well over ten thousand years before "moderns" totally replaced the Neanderthal, despite the recent evidence of some successful interbreeding.

There were separate developments in the human line, in other regions such as Southern Africa, that somewhat resembled the European and Western/Central Asian Neanderthals, but these people were not actually Neanderthals. One such example is Rhodesian Man (*Homo rhodesiensis*) who existed long before any classic European Neanderthals, but had a more modern set of teeth and arguably some *H. rhodesiensis* populations were on the road to modern *Homo sapiens sapiens*.

To date, no intimate connection has been found between these similar people and the Western/Central Eurasian Neanderthals, at least during the same time as classic Eurasian Neanderthals and *H. rhodesiensis* seems to have evolved separately and earlier than classic Neanderthals in a case of convergent evolution.

It appears incorrect, based on present research and known fossil finds, to refer to any fossil outside Europe or Western and Central Asia as a true Neanderthal. True Neanderthals had a known range that possibly extended as far east as the Altai Mountains, but not farther to the east or south and apparently not into Africa. At any rate, in Africa the land immediately south of the Neanderthal range was possessed by "modern" *H. sap.*, since at least 160,000 years before the present.

Classic Neanderthal fossils have been found over a large area, from northern Germany to Israel and Mediterranean countries like Spain and Italy in the south and from England and Portugal in the west to Uzbekistan in the east. This area probably was not occupied all at the same time. The northern border of their range, in particular, would have contracted frequently with the onset of cold periods. On the other hand, the northern border of their range as represented by fossils may not be the real northern border of the area they occupied, since Middle Palaeolithic-looking artifacts have been found even further north, up to 60° N, on the Russian plain. Recent evidence has extended the Neanderthal range by about 1,250 miles (2,010 km) east into southern Siberia's Altai Mountains.

Anatomy

Neanderthal anatomy was more robust than anatomically modern humans.

Behavior

Neanderthals were almost exclusively carnivorous and apex predators, however new studies do indicate that they had cooked vegetables in their diet. They made advanced tools, had a language (the nature of which is debated) and lived in complex social groups.

Genome

Early investigations concentrated on mitochondrial DNA (mtDNA), which, owing to strictly matrilineal inheritance and subsequent vulnerability to genetic drift, is of limited value in evaluating the possibility of interbreeding of Neanderthals with Cro-Magnon people.

In 1997, geneticists were able to extract a short sequence of DNA from Neanderthal bones from 30,000 years ago.

In July 2006, the Max Planck Institute for Evolutionary Anthropology and 454 Life Sciences announced that they would sequence the Neanderthal genome over the next two years. This genome is expected to be roughly the size of the human genome, three-billion base pairs and share most of its genes. It was hoped the comparison would expand understanding of Neanderthals, as well as the evolution of humans and human brains.

Svante Pääbo has tested more than 70 Neanderthal specimens. Preliminary DNA sequencing from a 38,000-year-old bone fragment of a femur found at Vindija Cave, Croatia, in 1980 showed *Homo neanderthalensis* and *Homo sapiens* share about 99.5% of their DNA. From mtDNA analysis estimates, the two species shared a common ancestor about 500,000 years ago. An article appearing in the journal *Nature* has calculated the species diverged about 516,000 years ago, whereas fossil records show a time of about 400,000 years ago. A 2007 study pushes the point of divergence back to around 800,000 years ago.

Edward Rubin of the Lawrence Berkeley National Laboratory in Berkeley, California, states recent genome testing of Neanderthals suggests human and Neanderthal DNA are some 99.5% to nearly 99.9% identical.

On 16 November 2006, Lawrence Berkeley National Laboratory issued a press release suggesting Neanderthals and ancient humans probably did not interbreed. Edward M. Rubin, director of the U.S. Department of Energy's Lawrence Berkeley National Laboratory and the Joint Genome Institute (JGI), sequenced a fraction (0.00002) of genomic nuclear DNA (nDNA) from a 38,000-year-old Vindia Neanderthal femur. They calculated the common ancestor to be about 353,000 years ago and a complete separation of the ancestors of the species about 188,000 years ago. Their results show the genomes of modern humans and Neanderthals are at least 99.5% identical, but despite this genetic similarity and despite the two species having coexisted in the same geographic region for thousands of years, Rubin and his team did not find any evidence of any significant crossbreeding between the two. Rubin said, "While unable to definitively conclude that interbreeding between the two species of humans did not occur, analysis of the nuclear DNA from the Neanderthal suggests the low likelihood of it having occurred at any appreciable level."

In 2008 Richard E. Green et al. from Max Planck Institute for Evolutionary Anthropology in Munich, Germany published the full sequence of Neanderthal mitochondrial DNA (mtDNA) and suggested "Neanderthals had a long-term effective population size smaller than that of modern humans." Writing in *Nature* about Green et al.'s findings, James Morgan asserted the mtDNA sequence contained clues that Neanderthals lived in "small and isolated populations and probably did not interbreed with their human neighbours."

In the same publication, it was disclosed by Svante Pääbo that in the previous work at the Max Planck Institute that "Contamination was indeed an issue," and they eventually realized that 11% of their sample was modern human DNA. Since then, more of the preparation work has been done in clean areas and 4-base pair 'tags' have been added to the DNA as soon as it is extracted so the Neanderthal DNA can be identified.

With 3 billion nucleotides sequenced, analysis of about 1/3rd showed no sign of admixture between modern humans and Neanderthals, according to Pääbo. This concurred with the work of Noonan from two years earlier. The variant of microcephalin common outside Africa, which was suggested to be of Neanderthal origin and responsible for rapid brain growth in humans, was not found in Neanderthals. Nor was the MAPT variant, a very old variant found primarily in Europeans.

However, an analysis of a first draft of the Neanderthal genome by the same team released in May 2010 indicates interbreeding may have occurred. "Those of us who live outside Africa carry a little Neanderthal DNA in us," said Pääbo, who led the study. "The proportion of Neanderthal-inherited genetic material is about 1 to 4 percent. It is a small but very real proportion of ancestry in non-Africans today," says Dr. David Reich of Harvard Medical School in Boston, who worked on the study. This research compared the genome of the Neanderthals to five modern humans from China, France, sub-Saharan Africa and Papua New Guinea. The finding is that about 1 to 4 percent of the genes of the non-Africans came from Neanderthals, compared to the baseline defined by the two Africans. This indicates a gene flow from Neanderthals to modern humans, i.e., interbreeding between the two populations. Since the three non-African genomes show a similar proportion of Neanderthal sequences, the interbreeding must have occurred early in the migration of modern humans out of Africa, perhaps in the Middle East. No evidence for gene flow in the direction from modern humans to Neanderthals was found. The latter result would not be unexpected if contact occurred between a small colonizing population of modern humans and a much larger resident population of Neanderthals. A very limited amount of interbreeding could explain the findings, if it occurred early enough in the colonization process.

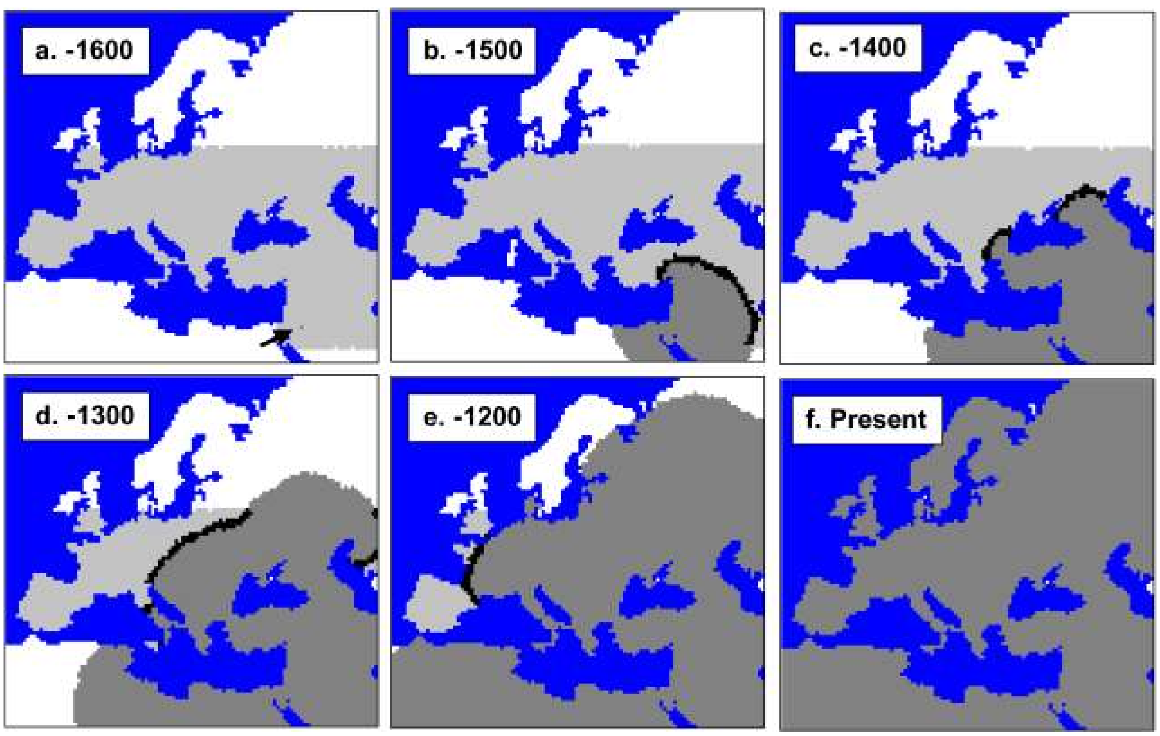
While interbreeding is viewed as the most parsimonious interpretation of the genetic discoveries, the authors point out they cannot conclusively rule out an alternative scenario, in which the source population of non-African modern humans was already more closely related to Neanderthals than other Africans were, due to ancient genetic divisions within Africa.

Among the genes shown to differ between present-day humans and Neanderthals were *RPTN*, *SPAG17*, *CAN15*, *TTF1* and *PCD16*.

Extinction hypotheses

The Neanderthals disappear from the fossil record after about 25,000 years ago. The last traces of Mousterian culture (without human specimens) have been found in Gorham's Cave on the remote south-facing coast of Gibraltar, dated 30,000 to 24,500 years ago. Possible scenarios are:

1. Neanderthals were a separate species from modern humans and became extinct (due to climate change or interaction with humans) and were replaced by *H. sapiens* moving into its habitat beginning around 80 kya. Competition from *H. sapiens* probably contributed to Neanderthal extinction. Jared Diamond has suggested a scenario of violent conflict and displacement.
2. Neanderthals were a contemporary subspecies that bred with *Homo sapiens* and disappeared through absorption (interbreeding hypothesis).



mtDNA-based simulation of modern human expansion in Europe starting 1600 generations ago. Neanderthal range in light grey.

As Jordan notes: "A natural sympathy for the underdog and the disadvantaged lends a sad poignancy to the fate of the Neanderthal folk, however it came about." Jordan, though, does say that there was perhaps interbreeding to some extent, but that populations that remained totally Neanderthal were likely out-competed and marginalized to extinction by the Aurignacians.

Climate change

About 55,000 years ago, the weather began to fluctuate wildly from extreme cold conditions to mild cold and back in a matter of a few decades. Neanderthal bodies were well suited for survival in a cold climate—their barrel chests and stocky limbs stored body heat better than the Cro-Magnons. However, the rapid fluctuations of weather caused ecological changes to which the Neanderthals could not adapt. The weather changes were so rapid that within a lifetime, plants and animals someone grew up with would be replaced by completely different plants and animals. Neanderthal's ambush techniques would have failed as grasslands replaced trees. A large number of Neanderthals would have died during these fluctuations, which peaked about 30,000 years ago.

Studies on Neanderthal body structures have shown that they needed more energy to survive than any other species. Their energy needs were up to 100-350 calories more per day comparing to projected anatomically modern human males weighing 68.5 kg and females 59.2 kg. When food became scarce, this difference may have played a major role in the Neanderthals' extinction.

Coexistence with H. sapiens

There is no longer certainty regarding the identity of the humans who produced the Aurignacian culture, even though the presumed westward spread of anatomically modern humans (AMHs) across Europe is still based on the controversial first dates of the Aurignacian. Currently, the oldest European anatomically modern *Homo sapiens* is represented by a robust modern-human mandible discovered at Peştera cu Oase (southwest Romania), dated to 34–36 thousand years ago. Human skeletal remains from the German site of Vogelherd, so far regarded as the best association between anatomically modern *Homo sapiens* and Aurignacian culture, were revealed to represent intrusive Neolithic burials into the Aurignacian levels and subsequently all the key Vogelherd fossils are now dated to 3.9–5.0 thousand years ago instead. As for now, the expansion of the first anatomically modern humans into Europe cannot be located by diagnostic and well-dated AMH fossils "west of the Iron Gates of the Danube" before 32 thousand years ago.

Consequently, the exact nature of biological and cultural interaction between Neanderthals and other human groups between 50 and 30 thousand years ago is currently hotly contested. A new proposal strives to resolve the issue by proposing the Gravettians rather than the Aurignacians as the anatomically modern humans who contributed to the Eurasian genetic pool after 30 thousand years ago. Correspondingly, the human skull fragment found at the Elbe River bank at Hahnöfersand near Hamburg was once radiocarbon-dated to 36,000 years ago and seen as possible evidence for the intermixing of Neanderthals and anatomically modern humans. It is now dated to the more recent Mesolithic.

Interbreeding hypotheses

An alternative to extinction is that Neanderthals were absorbed into the Cro-Magnon population by interbreeding. This would be counter to strict versions of the Recent African Origin, since it would imply that at least part of the genome of Europeans would descend from Neanderthals.

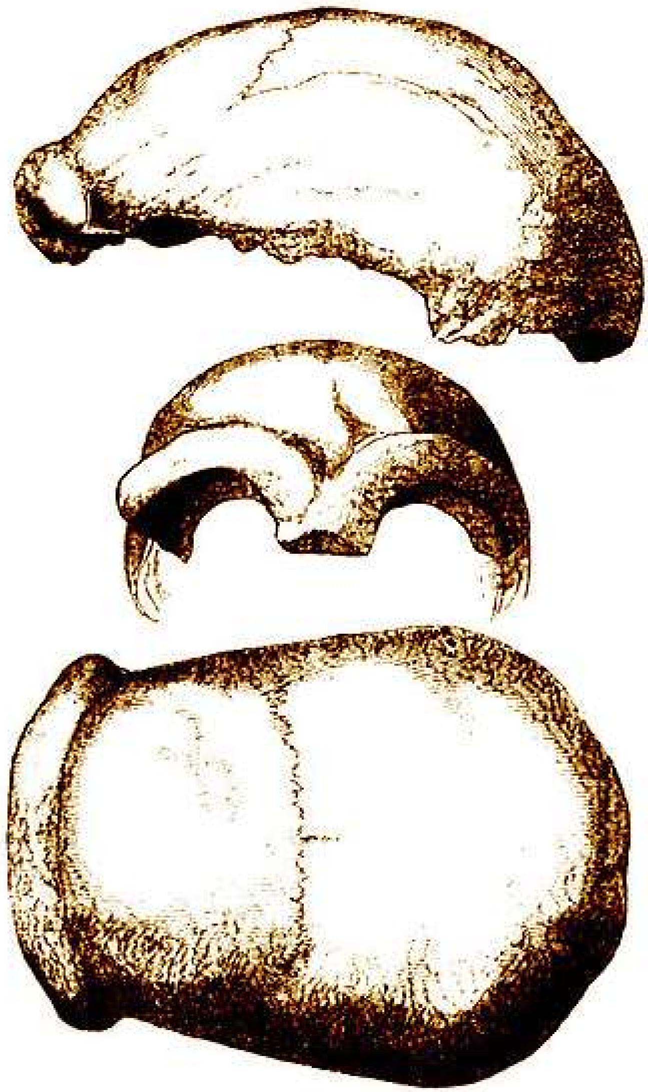
The most vocal proponent of the hybridization hypothesis is Erik Trinkaus of Washington University. Trinkaus claims various fossils as hybrid individuals, including the "child of Lagar Velho", a skeleton found at Lagar Velho in Portugal dated to about 24,000 years ago. In a 2006 publication co-authored by Trinkaus, the fossils found in 1952 in the cave of Peștera Muierii, Romania, are likewise claimed as hybrids.

An estimated 1 to 4 percent of the DNA in Europeans and Asians (i.e. French, Chinese and Papua probands) is non-modern and shared with ancient Neanderthal DNA rather than with Sub-Saharan Africans (i.e. Yoruba and San probands). The cause of this is unclear. It has been suggested it is due to interbreeding between Neanderthals and the ancestors of non-Africans after they left Africa, but this is not certain.

Specimens

The Ferrassie skull

- Neanderthal 1: Initial Neanderthal specimen found during an archaeological dig in August 1856. Discovered in a limestone quarry at the Feldhofer grotto in Neanderthal, Germany. The find consisted of a skull cap, two femora, the three right arm bones, two of the left arm bones, ilium and fragments of a scapula and ribs.
- La Chapelle-aux-Saints 1: Called the Old Man, a fossilized skull discovered in La Chapelle-aux-Saints, France, by A. and J. Bouyssonie and L. Bardon in 1908. Characteristics include a low vaulted cranium and large browridge typical of Neanderthals. Estimated to be about 60,000 years old, the specimen was severely arthritic and had lost all his teeth, with evidence of healing. For him to have lived on would have required that someone process his food for him, one of the earliest examples of Neanderthal altruism (similar to Shanidar I.)
- La Ferrassie 1: A fossilized skull discovered in La Ferrassie, France, by R. Capitan in 1909. It is estimated to be 70,000 years old. Its characteristics include a large occipital bun, low-vaulted cranium and heavily worn teeth.
- Le Moustier: A fossilized skull, discovered in 1909, at the archaeological site in Peyzac-le-Moustier, Dordogne, France. The Mousterian tool culture is named after Le Moustier. The skull, estimated to be less than 45,000 years old, includes a large nasal cavity and a somewhat less developed brow ridge and occipital bun as might be expected in a juvenile.



Type Specimen, Neanderthal 1

- Shanidar 1: Found in the Zagros Mountains in northern Iraq; a total of nine skeletons found believed to have lived in the Middle Paleolithic. One of the nine remains was missing part of its right arm; theorized to have been broken off or amputated. The find is also significant because it shows that stone tools were present among this tribe's culture. One was buried with flowers, showing that some type of burial ceremony may have occurred.

Chapter- 9

Homo Floresiensis

Homo floresiensis	
Fossil range: Late Pleistocene	

A cast of a *Homo floresiensis* skull, American Museum of Natural History

Scientific classification (disputed)	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Primates
Family:	Hominidae
Tribe:	Hominini

Genus:	*Homo*
Species:	***H. floresiensis***

Binomial name

†***Homo floresiensis***
Brown et al., 2004

Homo floresiensis ("**Flores Man**", nicknamed "hobbit") is a possible species, now extinct, in the genus *Homo*. The remains were discovered in 2004 on the island of Flores in Indonesia. Partial skeletons of nine individuals have been recovered, including one complete cranium (skull). These remains have been the subject of intense research to determine whether they represent a species distinct from modern humans and the progress of this scientific controversy has been closely followed by the news media at large. This hominin is remarkable for its small body and brain and for its survival until relatively recent times (possibly as recently as 12,000 years ago). Recovered alongside the skeletal remains were stone tools from archaeological horizons ranging from 94,000 to 13,000 years ago.

The discoverers (archaeologist Mike Morwood and colleagues) proposed that a variety of features, both primitive and derived, identify these individuals as belonging to a new species, *H. floresiensis*, within the taxonomic tribe of Hominini. Hominini currently comprises the extant species human (the only living member of the genus *Homo*), bonobo (genus *Pan*) and chimpanzee (genus *Pan*); their ancestors; and the extinct lineages of their common ancestor. The discoverers also proposed that *H. floresiensis* lived contemporaneously with modern humans (*Homo sapiens*) on Flores.

Doubts that the remains constitute a new species were soon voiced by the Indonesian anthropologist Teuku Jacob, who suggested that the skull of LB1 was a microcephalic modern human. Two studies by paleoneurologist Dean Falk and her colleagues (2005, 2007) rejected this possibility. Falk *et al.* (2005) has been rejected by Martin *et al.* (2006) and Jacob *et al.* (2006) and defended by Morwood (2005) and Argue, Donlon *et al.* (2006).

Two orthopedic researches published in 2007 both reported evidence to support species status for *H. floresiensis*. A study of three tokens of carpal (wrist) bones concluded there were similarities to the carpal bones of a chimpanzee or an early hominin such as *Australopithecus* and also differences from the bones of modern humans. A study of the bones and joints of the arm, shoulder and lower limbs also concluded that *H. floresiensis* was more similar to early humans and apes than modern humans. In 2009, the publication of a cladistic analysis and a study of comparative body measurements provided further support for the hypothesis that *H. floresiensis* and *Homo sapiens* are separate species.

Critics of the claim for species status continue to believe that these individuals are *Homo sapiens* possessing pathologies of anatomy and physiology. A second hypothesis in this category is that the individuals were born without a functioning thyroid, resulting in a type of endemic cretinism (myxoedematous, ME).

Discovery

Cave on Flores Island where the specimens were discovered

Flores Island in Indonesia, shown highlighted in red

The specimens were discovered on the Indonesian island of Flores by a joint Australian-Indonesian team of archaeologists in 2003 looking for evidence of the original human migration of *H. sapiens* from Asia to Australia. They were not expecting to find a new species and were surprised at the recovery of a nearly complete skeleton of a hominin they dubbed LB1 because it was unearthed inside the Liang Bua Cave. Subsequent excavations recovered seven additional skeletons, dating from 38,000 to 13,000 years ago. An arm bone provisionally assigned to *H. floresiensis* is about 74,000 years old. The specimens are not fossilized and have been described as having "the consistency of wet blotting paper"; once exposed, the bones had to be left to dry before they could be dug up.[:86]

Researchers hope to find preserved mitochondrial DNA to compare with samples from similarly unfossilised specimens of *Homo neanderthalensis* and *H. sapiens*.

Sophisticated stone implements of a size considered appropriate to the 1-meter-tall human are also widely present in the cave. The implements are at horizons from 95,000 to 13,000 years ago and are associated with (found in the same stratigraphic layer as) an elephant of the extinct genus *Stegodon* (which was widespread throughout Asia during the Quaternary), presumably the prey of LB1. They also shared the island with giant rats, Komodo dragons and even larger species of lizards. *Homo sapiens* reached the region by around 45,000 years ago.

Anatomy

The most important and obvious identifying features of *H. floresiensis* are its small body and small cranial capacity. Brown and Morwood also identified a number of additional, less obvious features that might distinguish LB1 from modern *H. sapiens*, including the form of the teeth, the absence of a chin and the lesser angle in the head of the humerus (upper arm bone). Each of these putative distinguishing features has been heavily scrutinized by the scientific community, with different research groups reaching differing conclusions as to whether these features support the original designation of a new species, or whether they identify LB1 as a severely pathological *H. sapiens*. The discovery of additional partial skeletons has verified the existence of some features found in LB1, such as the lack of a chin, but Jacob and other research teams argue that these features do not distinguish LB1 from local *H. sapiens* morphology. Lyras *et al.* have asserted, based on 3D-morphometrics, that the skull of LB1 differs significantly from all *H. sapiens* skulls, including those of small-bodied individuals and microcephalics and is similar to the skull of *Homo erectus* alone.

Small bodies

The first set of remains to have been found, LB1, was chosen as the type specimen for the proposed species. LB1 is a fairly complete skeleton, including a nearly complete cranium (skull), determined to be that of a 30-year-old female. LB1 has been nicknamed the *Little Lady of Flores* or "Flo".

LB1's height has been estimated at about 1.06 m (3 ft 6 in). The height of a second skeleton, LB8, has been estimated at 1.09 m (3 ft 7 in) based on measurements of its tibia. These estimates are outside the range of normal modern human height and considerably shorter than the average adult height of even the smallest modern humans, such as the Pygmies (< 1.5 m (4 ft 11 in)), Twa, Semang (1.37 m (4 ft 6 in) for adult women) of Africa, or the Andamanese (1.37 m (4 ft 6 in) for adult women). Body mass is generally considered more biophysically significant than length and by that measure, differences between modern pygmies and *Homo floresiensis* are even greater. LB1's body mass has been estimated at 25 kg (55 lb). This is smaller than that of not only modern *H. sapiens*, but also *H. erectus*, which Brown and colleagues have suggested is the immediate ancestor of *H. floresiensis*. LB1 and LB8 are also somewhat smaller than the australopithecines from three million years ago, not previously thought to have expanded beyond Africa. Thus, LB1 and LB8 may be the shortest and smallest members of the extended human family discovered thus far.

Aside from smaller body size, the specimens seem otherwise to resemble *H. erectus*, a species known to have been living in Southeast Asia at times coincident with earlier finds purported to be of *H. floresiensis*. These observed similarities form the basis for the suggested phylogenetic relationship. Controversially, the same team has reported finding material evidence on Flores (stone tools) of a *H. erectus* occupation dating back 840,000 years ago, but not remains of *H. erectus* itself, much less transitional forms.

To explain the small stature of *H. floresiensis*, Brown *et al.* have suggested that in the limited food environment on Flores, *H. erectus* underwent strong insular dwarfism, a form of speciation which has been observed in other species on Flores also – including a *Stegodon* elephant species on Flores. (This elephant, of normal size, emerged on the island by 750,000 years ago, replacing a dwarf *Stegodon* species that went extinct by 840,000 years ago.) This hypothesis has been criticized by Teuku Jacob and colleagues who argue that LB1 is similar to the midget humans who populate a Flores village, Rampasasa, – and who point out that size can vary substantially in pygmy populations. Contradictory evidence has emerged.

Small brains

Top view of a cast of the LB1 skull

In addition to a small body size, *H. floresiensis* had a remarkably small brain. The brain of the holotype LB1 is estimated to have had a volume of 380 cm^3 (23 cu in)), placing it at the lower range of chimpanzees or the extinct australopithecines. LB1's brain size is half that of its presumed immediate ancestor, *H. erectus* (980 cm^3 (60 cu in)). The brain to body mass ratio of LB1 lies between that of *H. erectus* and the great apes. Insular dwarfism has been posited to explain the brain size reduction.

An indicator of intelligence is the size of Brodmann's area 10, the dorsomedial prefrontal cortex, an area of the brain associated with self-awareness. LB1's region 10 is about the same size as that of modern humans, despite the much smaller overall size of the brain.

Notwithstanding the small brain of *H. floresiensis*, the discoverers have associated it with advanced behaviors. Their cave shows evidence of the use of fire for cooking and *Stegodon* bones associated with the hominins have cut marks. The hominin specimens have also been associated with stone tools of the sophisticated Upper Paleolithic tradition typically associated with modern humans, who have nearly quadruple the brain volume (1,310–1,475 cm^3 (80–90.0 cu in)) and 2.6 times greater body mass. Some of these tools were apparently used in the necessarily cooperative hunting of *Stegodon* by these hominins.

Additional features

Additional features used to argue that the finds come from a population of previously unidentified hominids include the absence of a chin, the relatively low twist of the arm bones and the thickness of the leg bones. The presence of each of these features has been confirmed by independent investigators but their significance has been disputed.

The forearm and pectoral girdle of *H. floresiensis* have been examined by Larson *et al.* (2007). Modern humans have the top of the bone twisted between 145 to 165 degrees to the plane of the elbow joint. For LB1, the twist was initially reported to be 110 degrees. Larson later revised this measurement to 120 degrees. This could be an advantage when arm-swinging, but it complicates activities associated with modern people, such as tool-making. As for the pectoral girdle of *H. floresiensis*, they studied a broken clavicle of LB1 and a shoulder blade of LB6. The clavicle was relatively short, which in combination with the shape of the shoulder blade and the low twist of the arm bone resulted in the shoulder being moved slightly forward, as if it was shrugged. Thus *H. floresiensis* could bend the elbow in the way modern people do and Larson concluded that it may have been able to make tools.

Tocheri *et al.* (2007) examined three carpal bones believed to belong to LB1. The shapes of these bones were claimed to differ significantly from the bones of the modern human wrist and to resemble the wrist of great African apes or *Australopithecus*.

The feet of *H. floresiensis* were unusually flat and unusually long in relation with the rest of the body. As a result, when walking, it would have to bend its knees further back than modern people do. This forced the gait to be high stepped and the creature was not able to walk very fast. The toes had an unusual shape and the big toe was very short.

Recent survival

The species is thought to have survived on Flores at least until 12,000 years before present, making it the longest lasting non-modern human, surviving long past the Neanderthals (*H. neanderthalensis*), which became extinct about 24,000 years ago.

Because of a deep neighboring strait, Flores remained isolated during the Wisconsin glaciation (the most recent glacial period), despite the low sea levels that united Sundaland. This has led the discoverers of *H. floresiensis* to conclude that the species, or its ancestors, could only have reached the isolated island by water transport, perhaps arriving in bamboo rafts around 100,000 years ago (or, if they are *H. erectus*, then about 1 million years ago). This idea of *H. floresiensis* using advanced technology and cooperation on a modern human level has prompted the discoverers to hypothesize that *H. floresiensis* almost certainly had language. This suggestion has been one of the most controversial of the discoverers' findings.

Local geology suggests that a volcanic eruption on Flores approximately 12,000 years ago was responsible for the demise of *H. floresiensis*, along with other local fauna, including the elephant *Stegodon*. Gregory Forth hypothesized that *H. floresiensis* may have survived longer in other parts of Flores to become the source of the *Ebu Gogo* stories told among the local people. The *Ebu Gogo* are said to have been small, hairy, language-poor cave dwellers on the scale of this species. Believed to be present at the time of the arrival of the first Portuguese ships during the 16th century, these creatures are claimed to have existed as recently as the late 19th century. Gerd van den Bergh, a paleontologist working with the fossils, reported hearing of the Ebu Gogo a decade before the fossil discovery. On the island of Sumatra, there are reports of a 1-1.5m tall humanoid, the Orang Pendek which might be related to *H. floresiensis*. Henry Gee, senior editor at *Nature* magazine, speculates that species like H.floresiensis might still exist in the unexplored tropical forest of Indonesia.

Some anthropologists do not believe the specimens represent a different species. Teuku Jacob, formerly chief paleontologist of the Indonesian Gadjah Mada University argued that they were members of "... a sub-species of *Homo sapiens* classified under the Austrolomelanesid race". He contended that the LB1 find is from a 25–30 year-old omnivorous subspecies of *H. sapiens*, probably a pygmy and that the small skull is due to the genetic disorder microcephaly, which produces a small brain and skull.

Scandal over specimen damage

In early December 2004, Teuku Jacob removed most of the remains from their repository, Jakarta's National Research Centre of Archaeology, with the permission of only one of the project team's directors and kept them for three months. Some scientists expressed the fear that important scientific evidence would be sequestered by a small group of scientists who neither allowed access by other scientists nor published their own research. Jacob returned the remains on February 23, 2005 with portions severely damaged and missing two leg bones to the worldwide consternation of his peers. Reports noted the condition of the returned remains; "[including] long, deep cuts marking the lower edge of the Hobbit's jaw on both sides, said to be caused by a knife used to cut away the rubber mould"; "the chin of a second Hobbit jaw was snapped off and glued back together. Whoever was responsible misaligned the pieces and put them at an incorrect angle"; and, "The pelvis was smashed, destroying details that reveal body shape, gait and evolutionary history" and causing the discovery team leader Morwood to remark "It's sickening, Jacob was greedy and acted totally irresponsibly". Jacob, however, denied any wrongdoing. He stated that the damages occurred during transport from Yogyakarta back to Jakarta despite the physical evidence to the contrary that the jawbone had been broken while making a mold of bones.

In 2005 Indonesian officials forbade access to the cave. Some news media, such as the BBC, expressed the opinion that the reason for the restriction was to protect Jacob, who was considered "Indonesia's king of palaeoanthropology", from being proven to be wrong. Scientists were allowed to return to the cave in 2007 shortly after the death of Jacob.

Microcephaly hypothesis

Prior to Jacob's removal of the fossils, a CT scan was taken of the skull and a virtual endocast of the skull (i.e., a computer-generated model of the skull's interior) of *H. floresiensis* was produced and analysed by Dean Falk *et al.* This team concluded that the brainpan was not that of a pygmy nor an individual with a malformed skull and brain.

In response, Weber *et al.* conducted a survey the same year comparing the computer model of LB1's skull with a sample of microcephalic human skulls, concluding that the skull size of LB1 falls in the middle of the size range of the human samples and is not inconsistent with microcephaly. Next to dispute the finding of Falk *et al.* (2005) were Martin *et al.* (2006), who objected to the failure to compare the model of LB1's skull with a typical example of adult microcephaly. Martin and his coauthors concluded that the skull was probably microcephalic, arguing that the brain is far too small to be a separate dwarf species; if it were, the 400-cubic-centimeter brain would indicate a creature only one foot in height, one-third the size of the discovered skeleton. Shortly thereafter, a group of scientists from Indonesia, Australia and the United States came to the same conclusion by examining bone and skull structure (Jacob (2006)).

A cast of LB1 (left) was compared to several microcephalic skulls, amongst which is that of the microcephalic (right) used by Henneman in his attempt to present LB1 as a microcephalic. Argue (2006) and Lyras (2008) contend the opposite.

Brown and Morwood countered by claiming that the skeptics had drawn incorrect conclusions about bone and skull structure and mistakenly attributed the height of *H. floresiensis* to microcephaly. Falk's team replied to the critics of their study (Falk *et al.* (2006)). Morphologist Jungers examined the skull and concluded that the skeleton displays "no trace of disease". Argue, Donlon, *et al.* (2006) rejects microcephaly and concludes that the finds are indeed a new species.

Falk *et al.* (2007) offered further evidence that the claims of a microcephalic *H. sapiens* were not credible. Virtual endocasts of an additional nine microcephalic brains and ten normal human brains were examined and it was found that the *floresiensis* skulls are similar in shape to normal human brains, yet have unique features which are consistent with what one would expect in a new species. The frontal and temporal lobes of the *floresiensis* brain were found to be highly developed, in strong contrast to the microcephalic brain and advanced in ways different from modern human brains. This finding also answered past criticisms that the *floresiensis* brain was simply too small to be capable of the intelligence required for the members of *H. floresiensis* to create the tools found in their proximity. Falk *et al.* (2007) conclude that the onus is now upon the critics that continue to claim microcephaly to produce a brain of a microcephalic that bears resemblance to the *floresiensis* brain.

Falk's argument was supported by Lyras et al. (2008) in that 3D-morphometric features of the skulls of microcephalic *H. sapiens* indeed fall within the range of normal *H. sapiens* and that the LB1 skull falls well outside this range. This was interpreted as proving that LB1 cannot, on the basis of either brain or skull morphology, be classified as a microcephalic *H. sapiens*.

In 2009, a study by Jungers et al. presented a statistical analysis of skull shapes of healthy modern humans, microcephalic humans and several ancient human species, as well as *H. floresiensis*. They showed that the three grouped separately, with *H. floresiensis* among the ancient humans, providing evidence that *H. floresiensis* is a separate species instead of a diseased modern human.

Laron syndrome hypothesis

The anatomist Gary D. Richards introduced a new skeptical hypothesis in June 2006: that the skeletons from Flores might be the remains of people who suffered from Laron syndrome, a genetic disorder first reported in 1966. The next year, a team including Laron himself published a paper arguing that the morphological features of *H. floresiensis* are essentially indistinguishable from those of Laron syndrome. The team said that to determine whether the *H. floresiensis* individuals had Laron syndrome would require testing their DNA for the presence of the defective genes, if samples of that DNA ever become available. Critics of the hypothesis have however pointed out that despite the low stature, people suffering from Laron syndrome look nothing like the *Homo floresiensis* remains, particularly in the anatomy of the cranial vault.

Endemic cretinism hypothesis

In 2008 Australian researchers Peter J. Obendorf, Charles E. Oxnard and Ben J. Kefford suggested that LB1 and LB6 suffered from myxoedematous (ME) endemic cretinism resulting from congenital hypothyroidism and that they were part of an affected population of *H. sapiens* on the island. This disease, caused by various environmental factors including iodine deficiency, is a form of dwarfism which can still be found among the local Indonesian population. Affected people, who were born without a functioning thyroid, have both small bodies and reduced brain size but their mental retardation and motor disability is not as severe as with neurological endemic cretins. According to the authors of the study, the critical environment could have been present on Flores approximately 18,000 years ago, the period to which the LB fossils are dated. They wrote that various features found on the fossils, such as enlarged pituitary fossa, unusually straight and untwisted tops of the upper arm bone and relatively thick limbs, are a sign of this diagnosis. The double rooted lower premolar and primitive wrist morphology can be explained in this way as well. The oral stories about strange human-like creatures may also be a record of cretinism.

Falk challenged the premise of Oberndorf *et al.* Studying computer tomography scans of LB1's pituitary fossa, she came to the conclusion that it is not larger than usual. Peter Brown declared that the remains of the pituitary fossa were very poorly preserved and no meaningful measurement was possible.

In 2010 Colin Groves compared the Flores bones with those of ten people who had had cretinism, focusing on anatomical features which are typical of the disease. He found no overlap and stated that he had put the claim to rest. Unfortunately this article remains unpublished and the published abstract is insufficient to judge the merits or demerits of this work. However, a more recent article by Oxnard, Obendorf and Kefford rejects Groves' argument and revives the cretinism hypothesis. Oxnard *et al* also criticise the cladistic analysis of Argue *et al.* (2009), stating that it is not logically possible for the analysis to conclude that the Liang Bua remains represent a separate species and not a pathology because the cladistics analysis assumes that they do not represent a pathology.

Bone structure

Cast of the entire LB1 specimen

The bone structure of *H. floresiensis*' shoulders, arms and wrists have been described as very different from modern humans, much closer to the bone structure of chimpanzees or an early hominin. This adds support to the idea that *H. floresiensis* is a separate species of early human rather than a modern human with a physical disorder.

Susan G. Larson *et al.* analyzed the upper limb of LB1. They found that in LB1 the angle of humeral torsion is much less than in modern humans. This had been previously studied by Richards et al., who declared that it is a sign of modern pygmy populations and T. Jacob et al., who pointed out that muscle attachments on the bone suggest LB1 had weak muscles which resulted in little development of humeral torsion. Larson *et al.* rejected Richards' conclusion, arguing that the humeral torsion of pygmy populations is usually similar to that of peoples of average stature. They argued that Richards *et al.* cited a 1972 paper which had studied a sample of six female Eastern Central African pygmies and this sample was too small to represent the whole population. Larson *et al.* also failed to find signs of microcephaly on the studied bones.

Larson *et al.* also studied the relatively short clavicle and the unusual formation of the pectoral girdle. They compared their finding with the skeleton of Nariokotome Boy (variously classified as *H. ergaster* or *H. erectus*) and suggested that the pectoral girdle of *H. floresiensis* was a transitional stage in human shoulder evolution.

While some specialists, including paleoanthropologist Russell Ciochon of the University of Iowa, supported the conclusion, others, including Eric Delson of Lehman College, City University of New York, pointed out that the recent sample of *H. floresiensis* individuals is too small and that Larson's research was based just on one shoulder bone.

Tocheri *et al.* (2007) (including Morwood, Larson and Jungers), compared three carpal bones believed to belong to LB1 with carpal bones of modern humans, some earlier hominids and African apes. They concluded that the carpals from the Liang Bua cave resembled ape carpal bones and were significantly different from the bones of *H. sapiens*, *Homo neanderthalensis* or even *Homo antecessor* and that they were comparable to carpal bones of *Australopithecus*. The carpal bones of *H. floresiensis* were found to lack features that evolved with ancestors of modern humans at least about 800,000 years ago. These features are already formed during embryogenesis and therefore Tocheri et al. argue that it is improbable that the shape of *H. floresiensis* wrist bones could be a result of a developmental disease.

This conclusion was challenged by Robert Martin, since Jacob's death the leading proponent of the microcephaly hypothesis and Alan Thorne. Martin noted that no research has been done on wrists of microcephalic people. Thorne maintained that the differences were small and that similar variation could occur with living modern humans. He also pointed out that the carpal bones had been found scattered in the cave and it was not certain that they all belonged to the same individual. Project leader Morwood countered that there were also other features, such as the stature, body proportions, brain size, shoulder, pelvis, jaw and teeth which suggested that *H. floresiensis* is a separate species that evolved in isolation on the island.