

Chapter 1.4. Origin of *Homo sapiens*

Chapter 1.4 considers anthropogenesis, the origin of our own species. Combining data on fossils with the results obtained by comparison of genomes and phenotypes of extant species elucidated the general course of evolution of the clade of placental mammals which eventually produced *Homo sapiens*. However, many details of this process and, more importantly, its driving forces, remain obscure. We do not know at what point our ancestors became unquestionably human and have no idea what selectively advantages this humanity conferred.

Section 1.4.1 deals with the position of primates among other mammals, and with their phylogeny and modern diversity, which comprises over 400 species. Cladogeneses that produced extant primates begun 60 - 80 mya, and family Hominidae, which contains humans and the six extant species of great apes, diverged from its sister clade Hylobatidae (gibbons), 19-25 mya. The last common ancestor of humans and our sister clade, chimpanzees, lived 6-9 mya.

Section 1.4.2 treats evolution of the human clade after the human-chimpanzee cladogenesis. Successive segments of the human lineage are referred to as species from genera *Ardipithecus*, *Australopithecus*, and *Homo*. Our ancestor were bipedal since at least 5.0 Ma, their brain size begun to increase 3.0 mya, and tools were made since at least 2.5 mya. Starting from 1.8 mya human lineage underwent several expansions out of its cradle, Africa, the last of which occurred ~0.08 mya and produced the diversity of modern humans outside Africa.

Section 1.4.3 reviews three lineages that branched off the lineage of modern humans in the course of the last 6 Ma but eventually went extinct: robust African hominids attributed to genus *Paranthropus*, *Homo erectus* that evolved outside Africa for almost 2 Ma, and *Homo neanderthalensis* that branched off ~0.5 mya. Obviously, we would never know about these closest relatives without fossils. Especially in the case of the neanderthals, we do not know why they went extinct, while our ancestors did not.

Chapter 1.4 completes the treatment of the chronology of life, mostly covered in Chapter 1.3, and is connected to applications of evolutionary biology to various aspects of the human condition, the subject of the Epilogue.

Section 1.4.1. Primates

Primates diverged from their closest relatives, tree shrews and flying lemurs, ~90 - 70 mya. Cladogeneses that produced the major clades of extant primates, Strepsirhini, Haplorhini, Platyrrhini, Catarrhini, Cercopithecoidea, and Hominoidea, occurred 80-30 mya. There are ~400 extant species of primates, and a number of important fossils that elucidate primate evolution have been discovered. *Homo sapiens* and the six of our closest extant relatives belong to the clade Hominidae, which diverged from its sister clade Hylobatidae (gibbons) ~25-19 mya. Divergence between the human clade and its sister chimpanzee clade occurred 6-9 mya, and the genotype of their last common ancestor can be mostly reconstructed, by comparison of genotypes of extant hominids.

1.4.1.1. Phylogeny and diversity of primates

Primates belong to the clade Euarchontoglires (Fig. 1.1.3.6a), which diverged into Glires (rodents and lagomorphs) and Euarchonta (Scandentia, Dermoptera, and Primates) in the Cretaceous, ~100 - 80 mya (Fig. 1.4.1.1a). Extant Scandentia comprise two families of tree shrews (20 species totally) and extant Dermoptera consist of only two species of flying lemurs (Fig. 1.4.1.1b). The ancestral lineage of Primates diverged from other Euarchonta 90 - 65 mya.

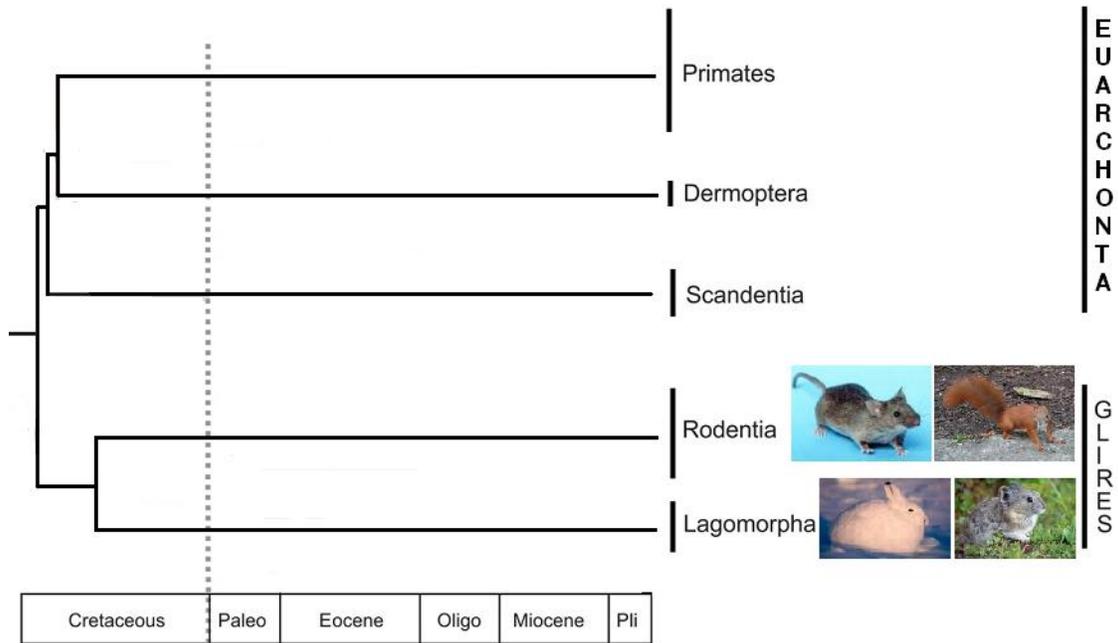


Fig. 1.4.1.1a. A likely phylogeny of Euarchontoglires (*Science* 318, 792, 2007). The relationships between Dermoptera, Scandentia, and Primates are still not fully certain (*Bio Essays* 31, 853, 2009).





Fig. 1.4.1.1b. Not-primate Euarchonta. (top) Tree shrews Scandentia: common tree shrew *Tupaia glis* (left) and the pen-tailed tree shrew *Ptilocercus lowii* (right). (bottom) Flying lemurs Dermoptera: colugo *Galeopterus variegatus* (left) and Philippine flying lemur *Cynocephalus volans* (right).

The relationships between major clades of Primates have been mostly resolved, but the dates of their divergences remain uncertain, although they very likely lay within the intervals shown in Fig. 1.4.1.1c. The sister clade of Strepsirrhini (lemurs and allies) is called Haplorrhini, the clade comprising Old World monkeys, gibbons, and great apes is called Catarrhini, and the clade comprising New World monkeys is called Platyrrhini. Strepsirrhini, Haplorrhini, Platyrrhini, and Catarrhini stand for wet-nosed, simple-nosed, broad-nosed, and narrow-nosed primates, respectively. A relatively old age of Primates is reflected in their widespread geographical distribution (Fig. 1.4.1.1d).

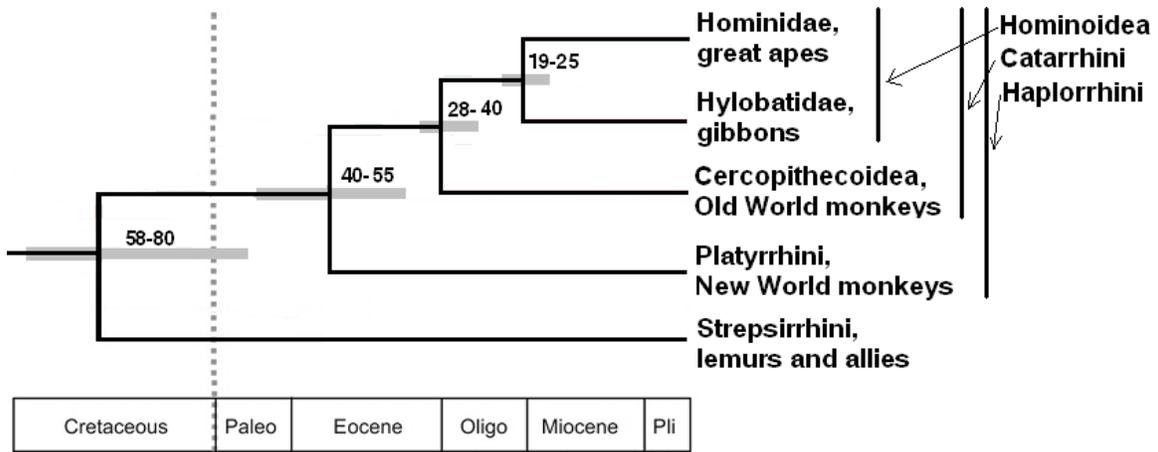


Fig. 1.4.1.1c. Phylogeny of the major clades of Primates (*Mol. Phyl. Evol.* 41, 384, 2006; *BMC Evolutionary Biology* 9:259, 2009).



Fig. 1.4.1.1d. The distribution of extant primates (<http://en.wikipedia.org/wiki/Primate>).

The basal clade of extant primates, Strepsirrhini, comprise ~140 species and live in Madagascar, where they are the only native primates, Southeast Asia, and Africa (Fig. 1.4.1.1e). ~130 of species of Platyrrhini inhabit Central and South America (Fig. 1.4.1.1f). Old World monkeys Cercopithecoidea, with approximately the same number of species, are native to Africa and Asia (Fig. 1.4.1.1g). All ~20 extant species of Hominoidea (gibbons Hylobatidae and Hominidae) lack tails. Over 10 species of Hylobatydae live in rainforests of Asia and Indonesia (Fig. 1.4.1.1h). Over 20 primate species are critically endangered.



Fig. 1.4.1.1e. Three species of Strepsirrhini: Mohol bushbaby *Galago moholi* (left), Black lemur *Eulemur macaco macaco* (center), and Golden potto *Arctocebus aureus* (right).



Fig. 1.4.1.1f. Three species of Platyrrhini: Brown spider monkey *Ateles hybridus* (left), Night monkey *Aotus lemurinus zonalis* (center), and Capuchin monkey *Cebus capucinus* (right).



Fig. 1.4.1.1g. Three species of Cercopithecoidea: Japanese snow monkey *Macaca fuscata* (left), Gelada *Theropithecus gelada* (center), Vervet monkey *Cercopithecus aethios* (right).



Fig. 1.4.1.1h. Three species of Hylobatidae: Lar gibbon *Hylobates lar* (left), siamang *Symphalangus syndactylus* (center), hoolock *Hoolock hoolock* (right).

Some key elements of the fossils record of Primates are summarized in Fig. 1.4.1.1i. This record begins from the stem-group Plesiadapiformes, which are known from a variety of fossils, spanning the range of ~65-40 mya and found in Europe, Asia, North America and Africa (Fig. 1.4.1.1j). Similarities of Plesiadapiformes and extant Primates include nails, instead of claws, and a number of dental traits. The earliest known

crown-group Primates, which probably belong to the stem-group of Strepsirrhini, are Adapiformes, who lived 60-20 mya in the same broad area as Plesiadapiformes (Fig. 1.4.1.1k). Some adapiforms were quite large and shared a number of similarities with Haplorrhini, apparently due to convergent evolution. Plausible stem Haplorrhini from a family Eosimiidae appeared in the fossil record in Asia 54 mya and in Africa 45 mya. Haplorrhini are known to have become diverse 34 Ma (Fig. 1.4.1.1l).

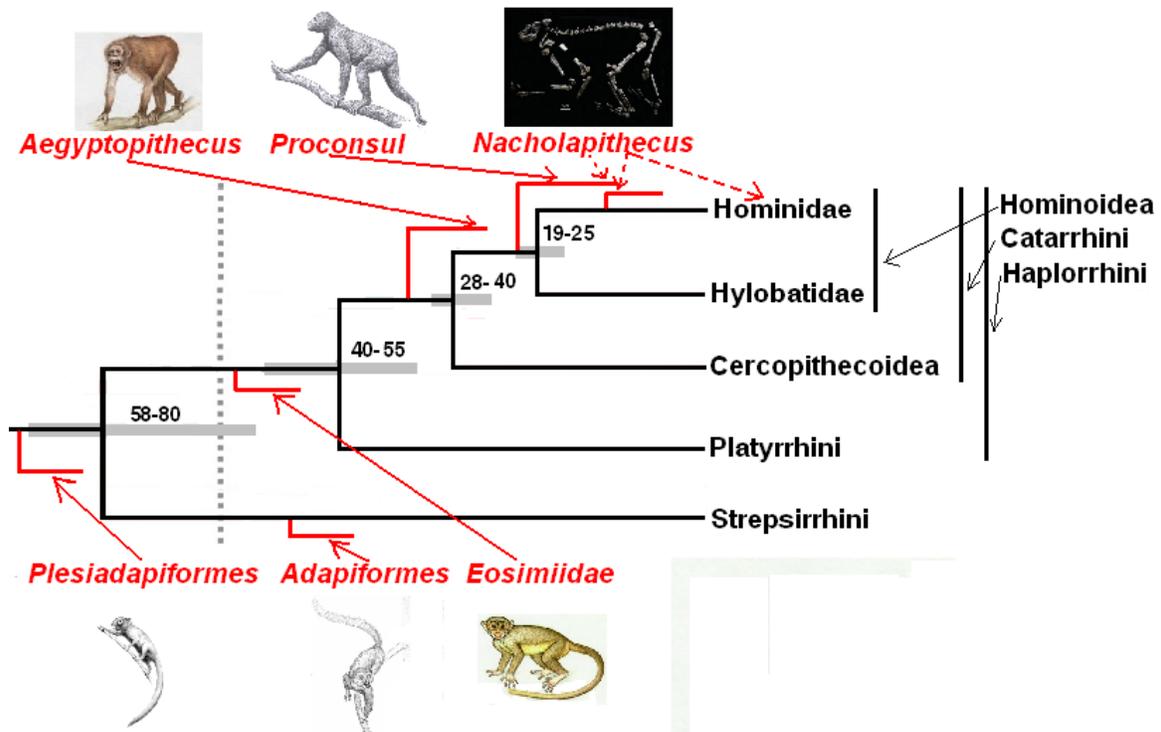


Fig. 1.4.1.1i. Likely phylogenetic positions of some key fossil primates relative to extant clades.

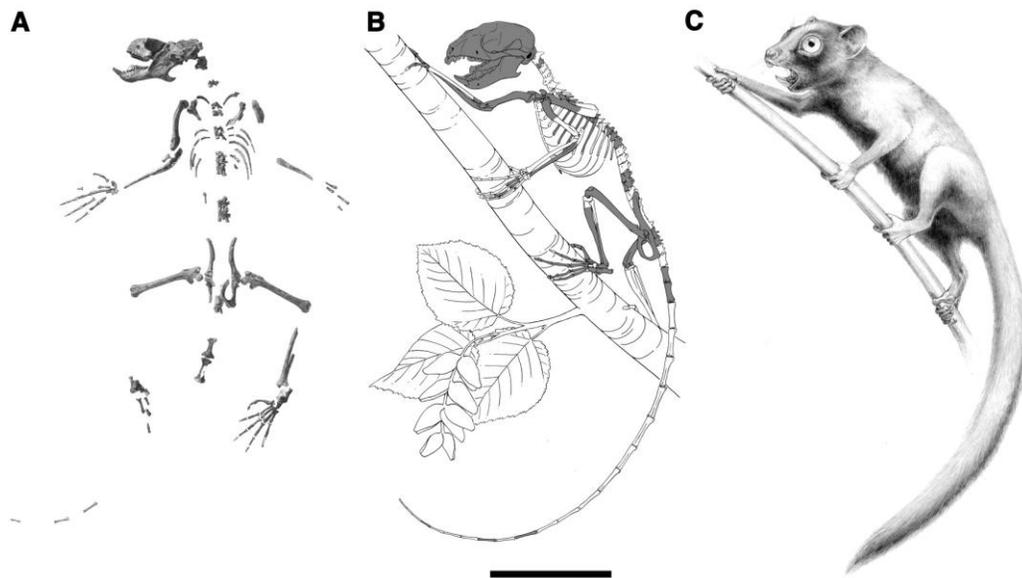


Fig. 1.4.1.1j. Skeleton (A) and reconstructions (B and C) of 55 Ma plesiadapiform *Carpolestes simpsoni*, found in Wyoming. *C. simpsoni* was a committed arborealist capable of grasping small-diameter supports with both its hands and feet, and might be similar to the common ancestor of extant Primates (*Science* 298, 1606, 2002; *J. of Human Evolution* 55, 1164, 2008).



Fig. 1.4.1.1k. *Darwinius masillae*, a 47 Ma old adapiform, found in Germany (*PLoS One* 4, e5723, 2009; *Nature* 461, 1040, 2009).



Fig. 1.4.1.11. Sample of North African ~34 Ma late Eocene monkeys from Fayum Quarry, Egypt (*Yearbook of Physical Anthropology* 48, 60, 2005; *PNAS* 105, 11093, 2008).

Fossils of a stem catarrhine species *Aegyptopithecus zeuxis* are known from the 29-30 Ma early Oligocene Jebel Qatrani Formation in Egypt. They include a well-preserved small female cranium which indicates strong sexual dimorphism (Fig. 1.4.1.1m). *A. zeuxis* had a brain-to-body mass ratio lower than that of living Haplorrhini. Thus, encephalization to some extent evolved independently in Platyrrhini and Catarrhini, and the relative brain size of the last common ancestor of crown Haplorrhini was probably strepsirrhine-like or even smaller.

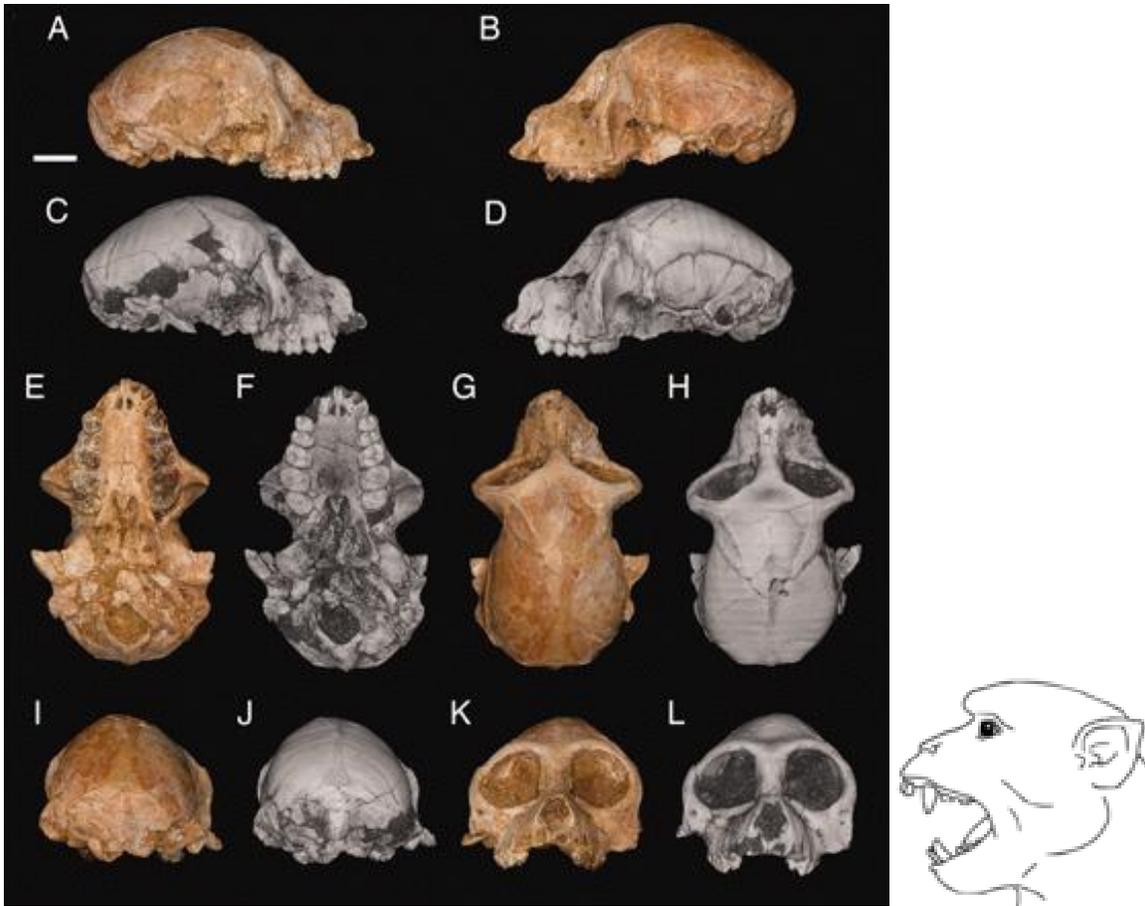


Fig. 1.4.1.1m. (left) Photographs (color) and 3D digital reconstructions (grayscale) of a female cranium of *A. zeuxis*. (*PNAS* 104, 8731, 2007). (right) A plausible reconstruction of this species.

A plausible stem hominoid genus *Proconsul* lived in African rainforests since 23 MA and its several species were generalized arboreal quadrupeds (Fig. 1.4.1.1n). Their brain-to-body mass ratio was slightly above those of extant Cercopithecoidea. Like all extant hominoids, *Proconsul* species lack tails, which is probably their synapomorphy. The clade of *Proconsul* may have survived for a long time, if it includes a 9.5 Ma *Samburupithecus kiptalami*. There was a substantial diversity of hominoids 17-14 mya: eight large-sized species have been described from fossils of that period found in Africa, Western Asia, and Europe (Fig. 1.4.1.1o), but their phylogenetic position is not yet clear. On the one hand, at least some of them may represent stem hominids or even crown hominids, more closely related to extant African hominids than to orangutans. On the

other hand, all of them could be stem hominoids like *Proconsul*. At least one of these hominoids, *Nacholapithecus kerioi*, was in many respects similar to *Proconsul* but differed from it, in particular, by large forelimbs, perhaps due to a larger role of vertical climbing in its behavior.



Fig. 1.4.1.1n. Fossils of likely stem hominoids *Proconsul helesoni* (left) and *Proconsul africanus* (middle) and reconstruction of *P. africanus* (right) (*Journal of Human Evolution* 46, 777, 2004).



Fig. 1.4.1.1o. Skeleton of an adult male of *Nacholapithecus kerioi*, large-sized hominoid form 15 Ma Aka Aiteputh Formation in Nachola, Northern Kenia (*Evolutionary Anthropology* 18, 103, 2009).

1.4.1.2. Hominidae

The phylogeny of hominids is shown in Fig. 1.4.1.2a. It includes 4 extant genera and 7 species (Fig. 1.3.3.4b), although the numbers of species within *Pongo* and *Gorilla* may be debatable. Let us briefly describe our closest living relatives (see Wikipedia for details).

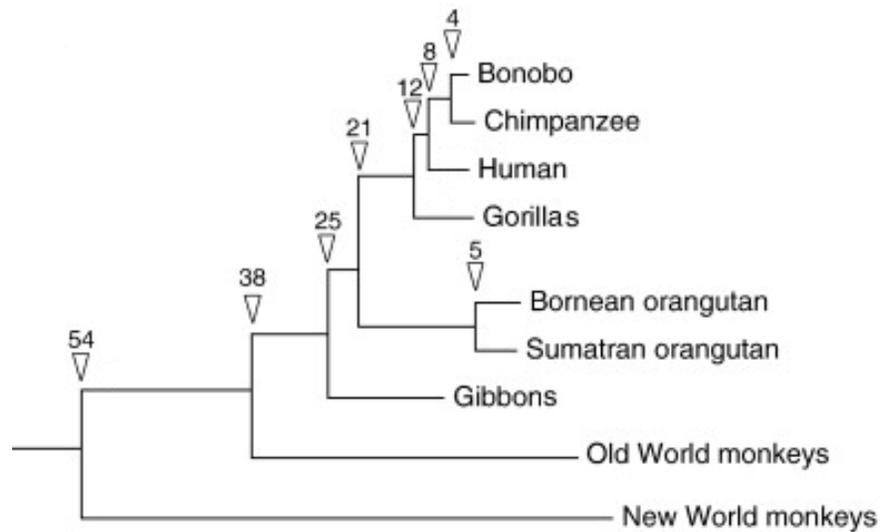


Fig. 1.4.1.2a. Hominid phylogeny. Numbers show the estimated times of different cladogeneses in Ma (*Gene* 421, 37, 2008). Corresponding estimates reported in other studies may be up to 25-50% smaller.

Orangutans *Pongo* are the only Asian living hominids. They inhabit rainforests on the islands of Borneo and Sumatra. Orangutans are the largest living arboreal animals, with standing height 1.2-1.5 m and weight 33-82 kg. Males are substantially larger than females. The age of maturity for females is approximately 12 years. Orangutans may live for up to 50 years in the wild. Their hands are similar to human hands, with four long fingers and an opposable thumb. Their feet have four long toes and an opposable big toe. Orangutans are solitary and can be fiercely territorial. Fruit makes up 65–90 percent of

the orangutan diet. Still, orangutans consume over 300 different food items that include young leaves, shoots, bark, insects, honey, and bird eggs. Bark is eaten as a last resort. Simple tools can be used. Babies stay with their mothers until they are about eight or nine years old. Bornean Orangutan *Pongo pygmaeus* is endangered and Sumatran Orangutan *Pongo abelii* is critically endangered.

Gorillas *Gorilla* are the largest of the living primates. They inhabit the forests of central Africa, and are ground-dwelling and predominantly herbivorous. Gorillas walk on all fours using their knuckles for support with their hands clenched, a form of locomotion called knuckle-walking. Adult males can be up to 1.75 m in height and up to 200 kg in weight, adult females are averaging about 1.4 m and 100 kg. Gorillas spend most of the day eating, their diet consists mostly of fruits, leaves, and shoots, and can use tools. Females mature at 10–12 years (earlier in captivity); males at 11–13 years. Infants stay with their mothers for 3–4 years. Lifespan is between 30–50 years. Gorillas mostly live in groups of 5-30, each led by a mature male (silverback). Both species of gorilla, Western Gorilla *Gorilla gorilla* and Eastern Gorilla *Gorilla beringei* are endangered, and have been subject to intense poaching for a long time.

Chimpanzees *Pan* inhabit tropical forests and wet savannas of Western and Central Africa. The male common chimp is up to 1.7 m (up to 5.6 ft) high when standing, and weighs as much as 70 kg (154 lb); the female is somewhat smaller. Chimpanzees use their long, powerful arms for climbing in trees. On the ground, chimpanzees usually move by knuckle-walking. However, they can also walk upright on two legs when carrying objects with their hands and arms. Chimpanzees reach puberty at an age of between 8 and 10 years and rarely live past the age of 40 in the wild. The Common Chimpanzee *P. troglodytes* has an omnivorous diet, a troop hunting culture based on beta males led by an alpha male, and highly complex social relationships. The Bonobo *P. paniscus* has a mostly frugivorous diet and an egalitarian, nonviolent, matriarchal, sexually receptive behavior. Evidence for "chimpanzee spirituality" includes display of mourning, "incipient romantic love", "rain dance", appreciation of natural beauty such as a sunset over a lake, curiosity and respect towards wildlife (such as the python, which is neither a threat nor a food source to chimpanzees), empathy toward other species (such as

feeding turtles) and even "animism" or "pretend play" in chimps cradling and grooming rocks or sticks. Both chimpanzee species are endangered.

Fossil record of the crown group Hominidae includes representatives from several clades. Asian *Sivapithecus* and *Gigantopithecus* belong to the clade of modern orangutans. Several species of *Sivapithecus* lived between 13 and 8 Ma (Fig. 1.4.1.2b). The genus *Gigantopithecus* went extinct not earlier than 0.3 mya, and one of its species, *G. blacki* was the largest ape known, standing up to 3 meters and weighting up to 540 kg.

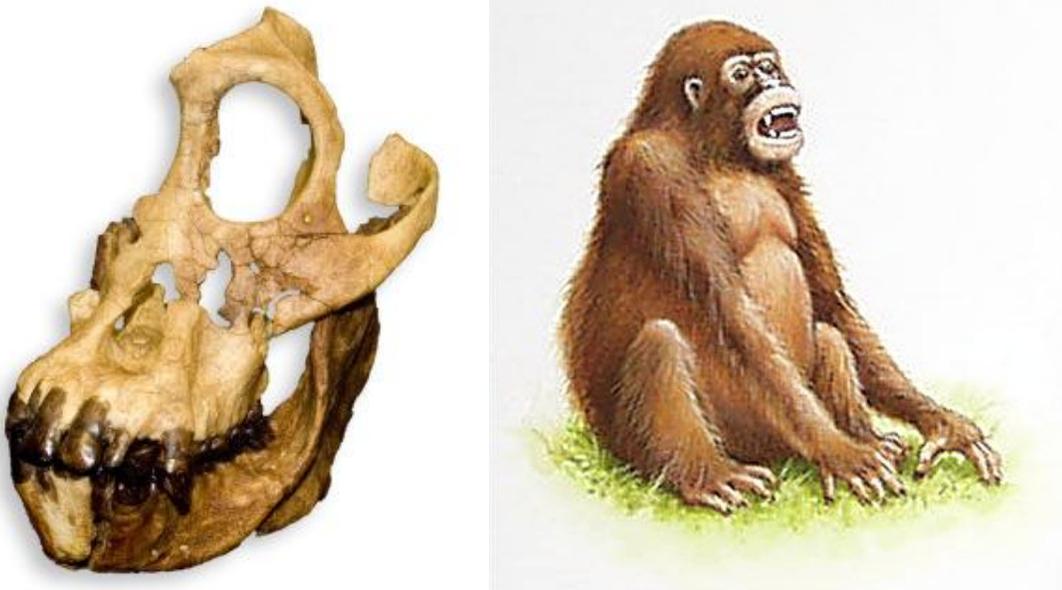


Fig. 1.4.1.2b. Fossil cranium and a reconstruction of *Sivapithecus indicus*.

Also, a number of fossil large great apes may be close to the common ancestor of African hominids, gorillas, chimpanzees, and humans. They include 10.5 - 10.0 Ma *Chororapithecus abyssinicus* from the Chorora Formation at the southern margin of the Afar rift; 9.9-9.8 Ma *Nakalipithecus nakayamai* from Nakali, Kenya; and 9.6-8.7 Ma *Ouranopithecus macedoniensis* from Greece. Fossils available so far are insufficient for definite conclusions (Fig. 1.4.1.2c). Still, *C. abyssinicus* may be a basal member of the *Gorilla* clade, and other species may represent lineages that branched off before the divergence of extant African hominids.

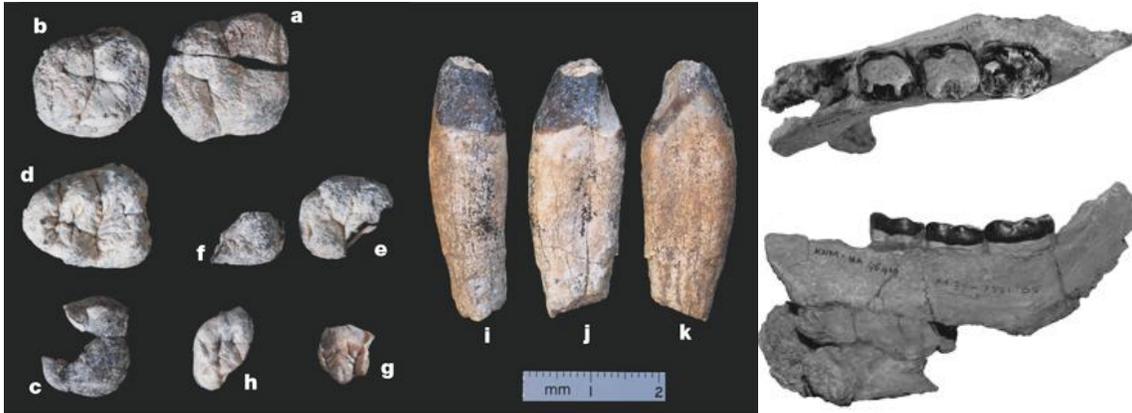


Fig. 1.4.1.2c. (left) Teeth of *Chororapithecus abyssinicus* (*Nature* 448, 921, 2007). (right) Right mandible of *Nakalipithecus nakayamai* (*PNAS* 104, 19220, 2007).

1.4.1.3. *The human-chimpanzee clade*

The exact time of the cladogenesis that produced chimpanzee and human clades remains unknown, although this very likely happened between 6 and 8 Ma (and definitely between, say, 5 and 11 Ma). There are no reasons to doubt that this cladogenesis occurred in Africa. To understand evolution of the human (and the chimpanzee) clade after this cladogenesis, it is essential to know the genotype and phenotype of their last common ancestor (HCLCA). Fossils that can shed light on this issue are *Ardipithecus* (*Sahelanthropus*) *tchadensis* and *Ar. (Orrorin)* *tugenensis*. However, they more likely belong to the human clade, and will thus be considered in Section 1.4.2. All members of the human clade past HCLCA are referred to as hominins (members of a tribe Hominini).

Parsimony-based ancestral reconstructions make sense only if we assume that evolution, at the scale of differences between the extant species which we compare, was slow (Section 1.1.3.3). In the case of human-chimpanzee (say, *P. troglodytes*) comparison, this is generally true at the level of genotypes, because there are only 13 individual genetic differences between human and chimpanzee genomes per each 1000 positions of their alignment. For reconstructing the HCLCA genome, orangutans may be a better outgroup than gorillas, because the cladogeneses that produced gorilla and chimpanzee+human clades and chimpanzee and human clades occurred too close to each other. Thus, some human-chimpanzee differences may be due to variation that persisted within the chimpanzee+human lineage since the time when the gorilla lineage branched

off, which would violate the assumption of a tree-like phylogeny (Fig. 1.1.3.5a). In contrast, orangutan diverged much earlier, but is still close enough to humans and chimpanzees genetically (Fig. 1.3.3.4b) to apply the principle of maximal parsimony.

By analyzing human-chimpanzee-orangutan genome alignment (Fig. 1.4.1.3a), we can with high confidence identify the ancestral state ("polarize") over 95% of individual human-chimpanzee genetic differences. A little less than 50% of these differences are due to changes in the human lineage, because at the sequence level the chimpanzee lineage evolved a little faster. Parsimony obviously cannot work when orangutan, chimpanzee, and human genomes all possess different states of a particular trait (for example, when at some position of the alignment, they carry nucleotides A, T, and G, respectively), but such situations are rare.

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Fig. 1.4.1.3a. An alignment of orthologous regions of intron 1 of an axon guidance receptor 2 from human (*Homo sapiens*), Common chimpanzee (*Pan troglodytes*), and Bornean orangutan (*Pongo pygmaeus*) genomes. Changes (two) that occurred, after human-chimpanzee cladogenesis, in the human lineage are in red, changes (one) in the chimpanzee lineage are in blue, and changes in the orangutan lineage, after the (human,chimpanzee)-orangutan cladogenesis, are in green.

It is also possible to reconstruct the human-chimpanzee ancestral genotype at the level of chromosomes. The haploid chromosome number is 24 in all extant hominids, except humans, who have 23 chromosomes. Comparison of sequences demonstrates that human chromosome 2 is a product of a recent telomere-to-telomere fusion of two ancestral chromosomes; in fact, the telomere sequences are still clearly identifiable within human chromosome 2.

Still, these genome-level analyses are not of much help for reconstructing HCLCA phenotype, unless one tries to synthesize its genotype artificially and to produce the corresponding animal, because too little is known about genotype - phenotype maps. Despite the overall similarity of human and chimpanzee genomes, there still are ~30,000,000 individual differences, mostly single-nucleotide substitutions but also some long deletions and insertions, between them. Most of these differences certainly have (almost) no impact on the phenotype, but we currently have no idea how many changes need to be introduced into the genotype of a chimpanzee to convert it into a passable human - 30, 3,000, or 3,000,00.

Parsimony can also be applied directly to phenotypes, but with much less confidence than to genotypes. Indeed, a phenotypic trait depends on very many genes, and, therefore, at least some phenotypic traits can diverge substantially even between genetically very similar species. Clearly, humans and chimpanzees possess, on top of

their profound similarity, a lot of striking morphological and behavioral differences. Above the neck, humans and chimpanzee differ by cranial capacity, size of the whole brain and relative sizes of its parts, prominence of brow ridges, jaw and teeth morphology, and many other traits (Fig. 1.4.1.3b). Below the neck, humans are characterized by shorter arms, much less developed musculature, wider pelvic outlet in women, adaptations of pelvis and legs to bipedal locomotion, *etc.* Differences between humans and chimpanzees in cognitive and linguistic abilities are even more profound.

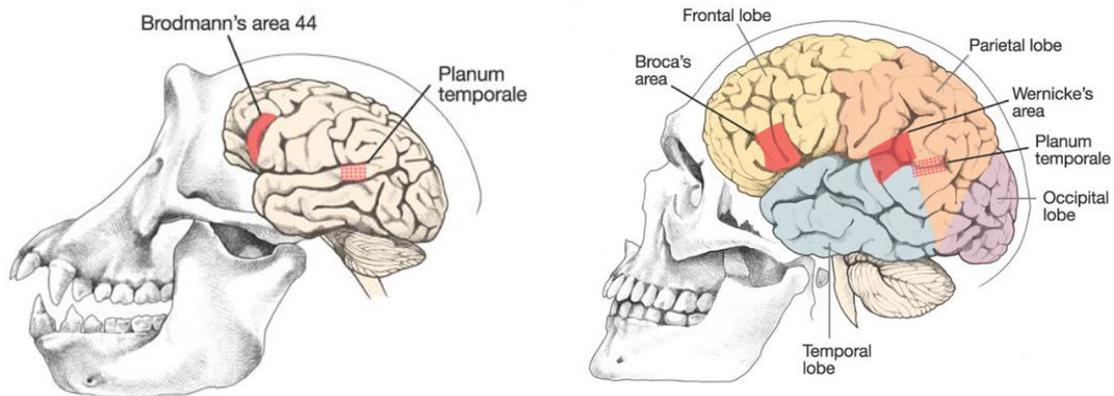


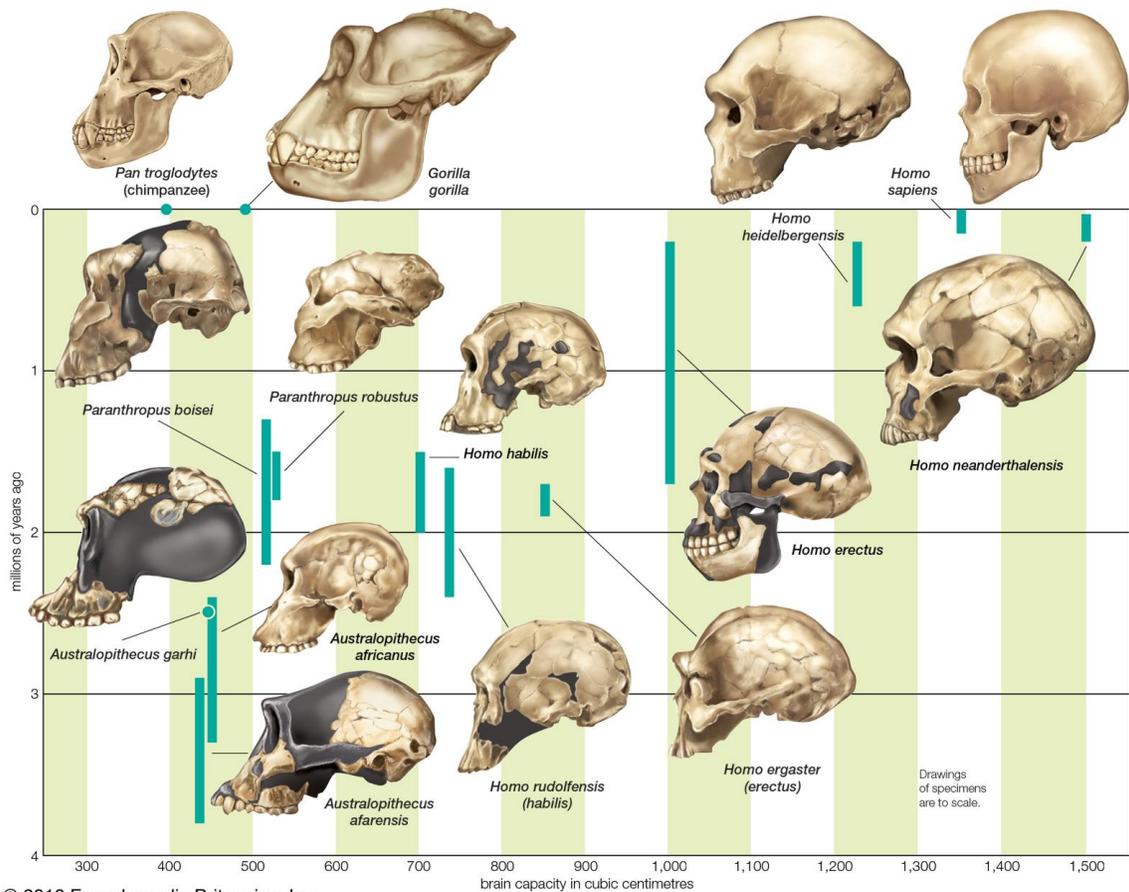
Fig. 1.4.1.3b. Comparative anatomy of chimpanzees and humans. (*Nature* 422, 849, 2003).

Still, it is probably safe to assume, from comparing average cranial capacities of gorillas (500 cm^3), chimpanzees (400 cm^3) and humans (1350 cm^3), that HCLCA had a relatively small brain, so that the brain size increased later in the human lineage. Similarly, we can be reasonably confident that HCLCA could not write poetry or play the violin. However, in other cases the application of parsimony is more dubious. For example, it seems possible that gorillas and chimpanzees acquired knuckle-walking independently, due to parallel or even convergent evolution, so that HCLCA could be bipedal.

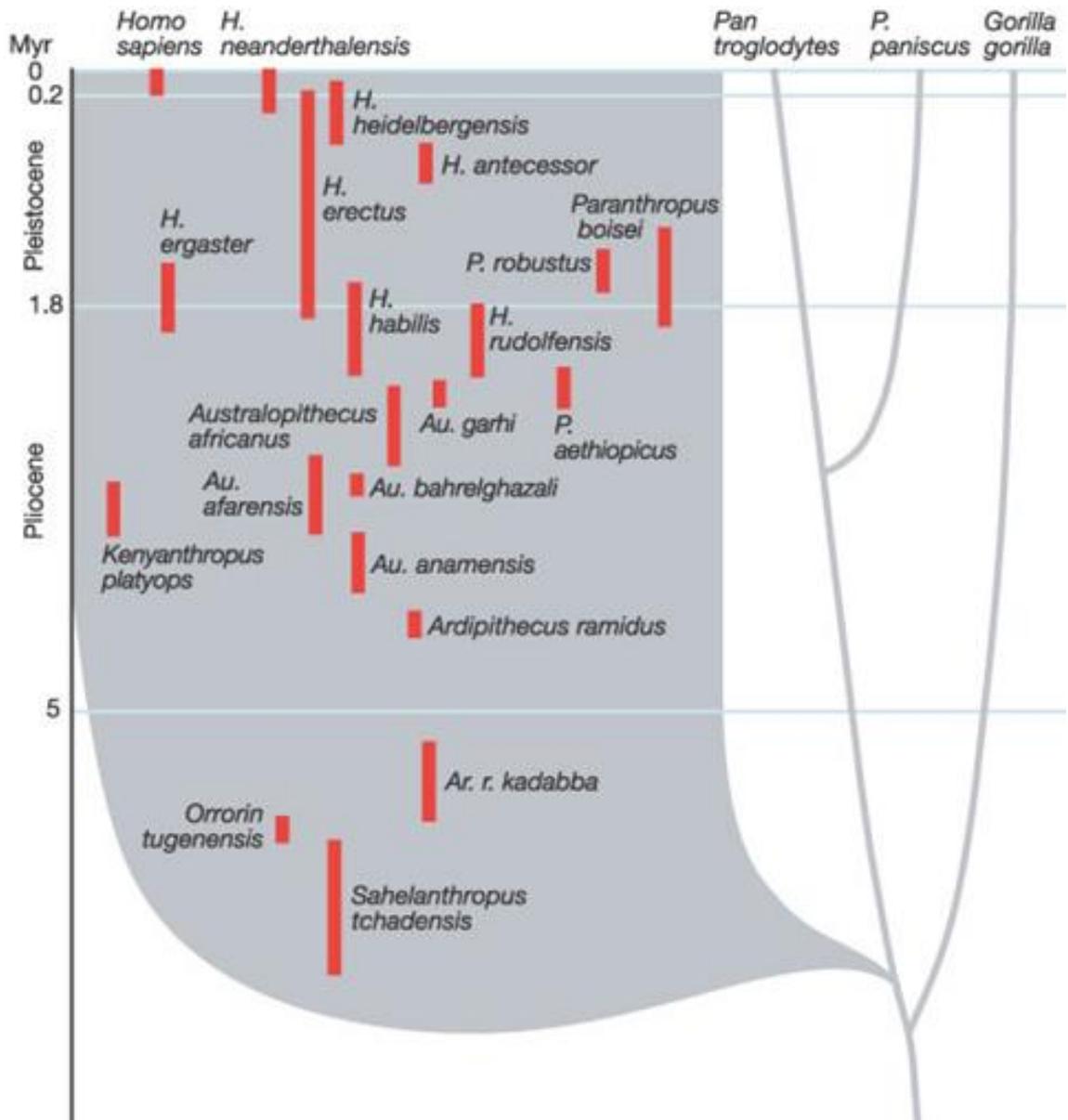
Even if a particular change can be confidently assigned to the lineage, comparison of extant species cannot tell us at which moment this change occurred. Similarly, such comparison does not reveal the order in which changes of different traits occurred. For example, without fossils we would probably never know whether in the human lineage cranial capacity began to increase before or after changes in the hand morphology.

Thus, at least at the level of phenotypes, our understanding of the last step of human evolution is based mostly on fossils. Fossil record of the chimpanzee clade is very poor and limited to the last ~0.5 Ma (*Nature* 437, 105, 2005). In contrast, there are many known fossils that definitely or plausibly belong to the human clade. Fig. 1.4.1.3c presents an overview of these fossils and summarizes them phylogenetically in the simplest way possible, *i. e.* by assuming only the minimal necessary number of cladogeneses within the human clade and the minimal number of coexisting lineages at each moment of time. The real story might be even more complex, and extra cladogeneses may be necessary to accommodate future discoveries.

Subdividing an evolving lineage into segments, referred to by different generic and specific Latin names, is bound to be arbitrary. Clearly, the high number of genera and species proposed for members of the human clade (Fig. 1.4.1.3c, middle) cannot be justified biologically, and is simply due to a tendency to give each prominent fossil its own name. I mostly follow (Fig. 1.4.1.3c, bottom) the lumping taxonomy proposed in (*Journal of Anatomy* 212, 354, 2008), and subdivide the lineage which directly led to modern humans into just 3 segments, with generic names *Ardipithecus* (7.0 - 4.3 Ma), *Australopithecus* (4.3 - 2.4 Ma) and *Homo* (2.4 Ma - present). Within these segments, however, I will keep the commonly used specific names, simply as labels for recognizing different important fossils.



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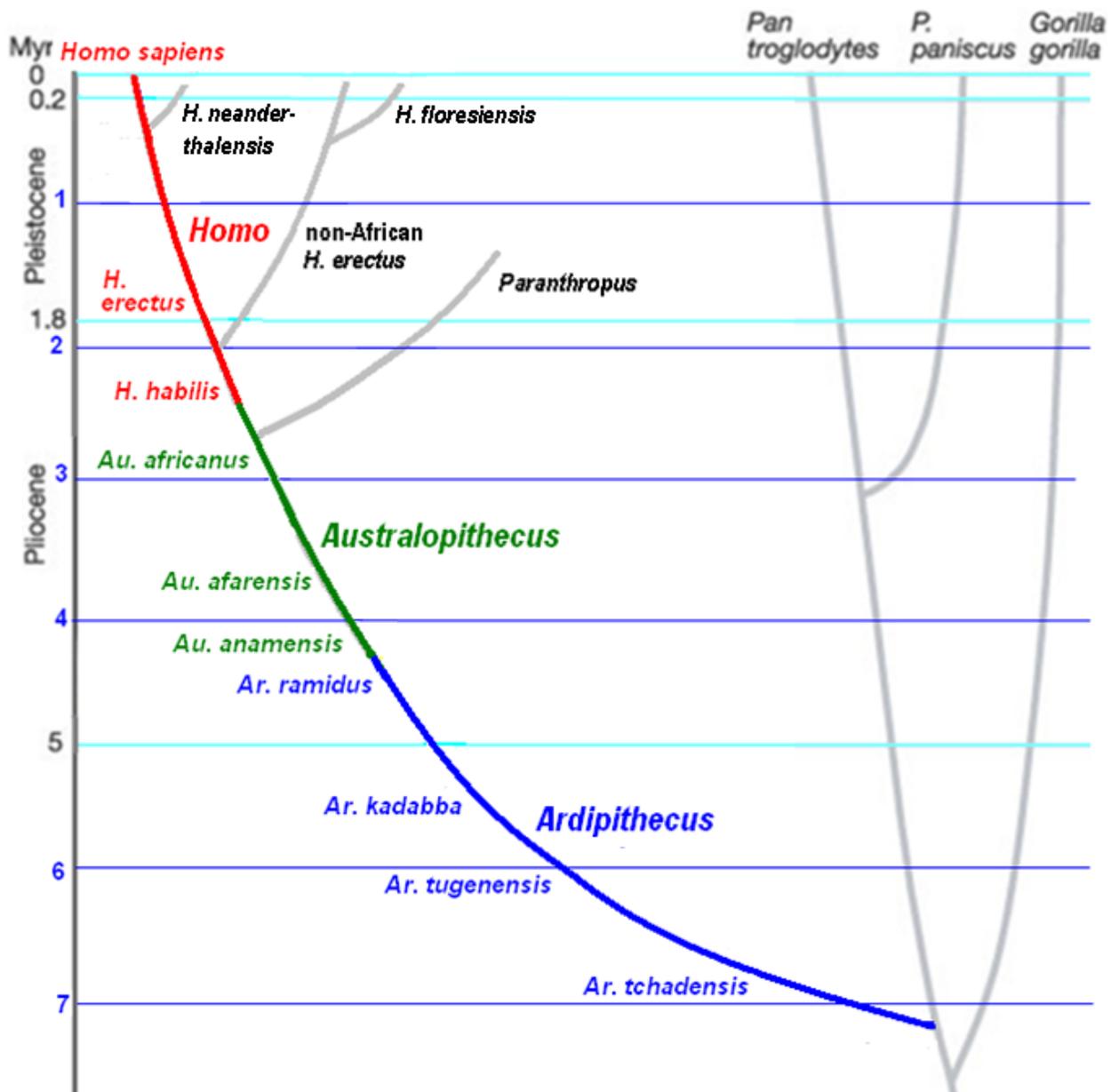


Fig. 1.4.1.3c. (top, middle) Summary of data on fossils that definitely or plausibly belong to the human clade after HCLCA. (bottom) The simplest phylogenetic tree that may be consistent with these data, and the taxonomy adopted here (*Journal of Anatomy* 212, 354, 2008).

Section 1.4.2. The last 7 Ma of the human lineage

The lineage that led to modern humans from the HCLCA can be arbitrarily subdivided into successive *Ardipithecus*, *Australopithecus*, and *Homo* segments. The

cranial capacity in our lineage originally was $\sim 350 \text{ cm}^3$, slightly less than in modern chimpanzees, and originally increased slowly, reaching only $\sim 450 \text{ cm}^3$ by 2.5 mya, after which time it began to increase rapidly towards the modern human value of $\sim 1400 \text{ cm}^3$. In contrast, bipedality evolved very early, before 5.0 mya, and 4.0 mya the feet of our ancestors became non-grasping. Teeth and jaws were not large initially, but their size increased 4.4 - 2.5 mya, only to become smaller again later. This may be caused by the onset of usage of primitive stone tools, documented from ~ 2.5 mya. After ~ 1.5 mya, stone tools became much more sophisticated. Fossils younger than 0.5 Ma can be comfortably attributed to *H. sapiens*. Out-of-Africa expansion which established the global range of our species occurred ~ 70 kya.

1.4.2.1. *Ardipithecus*

The ~ 7.0 - 4.3 Ma segment of the human lineage will be referred to as genus *Ardipithecus* ("ardi" = ground or floor in Afar language). The known fossil record of this segment until 4.4 Ma is rather poor, and consists of a small number of enigmatic and incomplete fossils. The first of them is ~ 7 Ma *Ar. tchadensis* (originally described as *Sahelanthropus tchadensis*), known from nearly-complete cranium (Fig. 1.4.2.1a) and jaw fragments of several individuals, all found in Central Africa in Chad. *Ar. tchadensis* had thick brow ridges and cranial capacity of $\sim 360 \text{ cm}^3$, similar to that of modern chimpanzees (Fig. 1.4.1.3c), but also had many substantial differences from them. It was probably be close to the HCLCA, possibly, but not definitely, belonging to the human clade. Anatomy of the cranium suggests that *Ar. tchadensis* was bipedal and walked upright, although such conclusions cannot be firm without postcranial bones, which are currently absent.

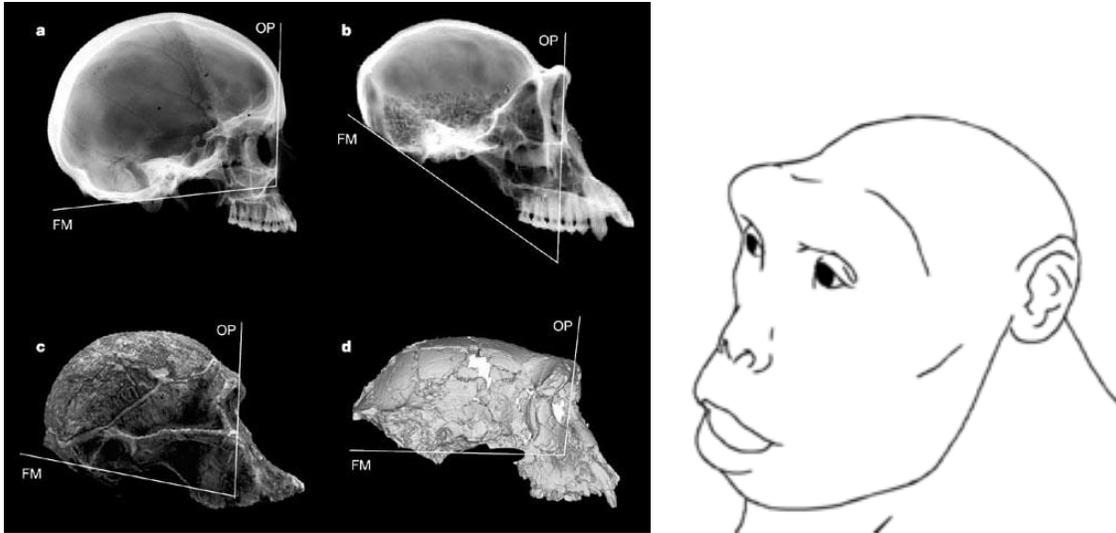


Fig. 1.4.2.1a. Comparison of craniums of: a, *Homo sapiens*; b, *Pan troglodytes*; c, *Australopithecus africanus* (see below); and d, *Ardipithecus tchadensis* (*Nature* 434, 755, 2005).

The second-oldest fossils that likely belongs to the human clade are ~ 6 Ma teeth and fragments of leg and arm bones found in Kenya and referred to as *Ar. tugenensis* (originally, *Orrorin tugenensis*). Morphology of its femur (thighbone) provides the first postcranial evidence of bipedality in the human clade, and indicates, together with its primitive dental morphology, that *Ar. tugenensis* may belong directly to the ancestral lineage of modern humans (Fig. 1.4.2.1b).

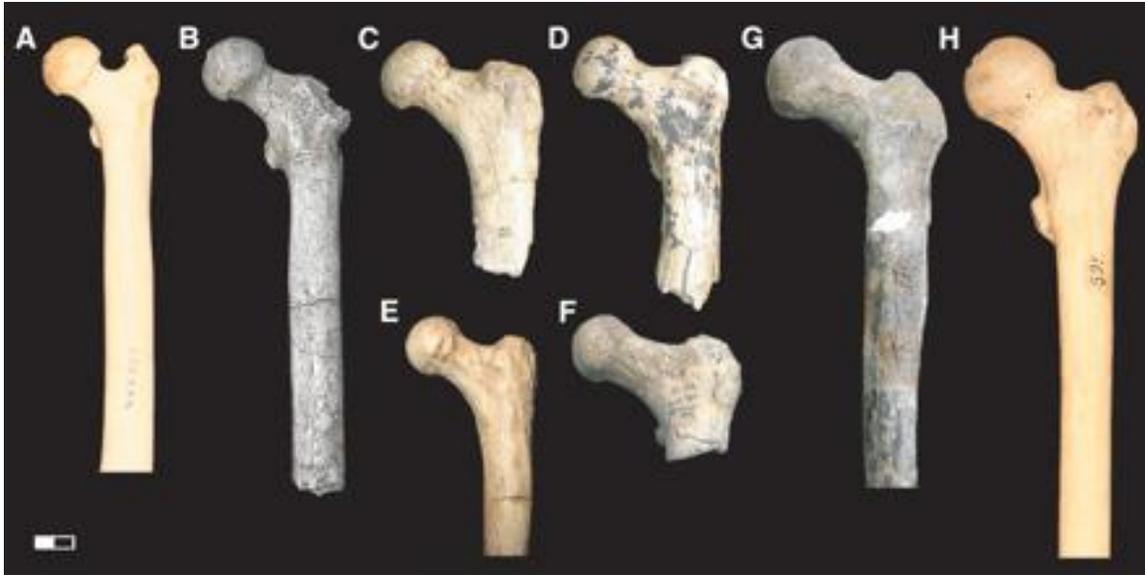


Fig. 1.4.2.1b. Comparisons among femora of (A) *P. troglodytes*, (B) *Ar. tugenensis*, (C and D) *Paranthropus robustus* (see below), (E) *Australopithecus afarensis* (see below), (F) *Paranthropus boisei* (see below), (G) early *Homo*, and (H) modern *H. sapiens*. Like other early fossil femora from the human clade (C to F), *Ar. tugenensis* femur (B) is distinct from those of modern humans (H) and great apes (A) in having a long, anteroposteriorly narrow neck and wide proximal shaft. Scale bar, 2 cm. (*Science* 307, 845, 2005; 319, 1662, 2008).

The next fossil from the *Ardipithecus* segment of the human lineage, *Ar. kadabba*, is the first of eight kinds of fossils, spanning the time interval from ~6.0 to 0.08 Ma, which belong to the human clade and were found in the Middle Awash area of the Ethiopian Afar rift (Fig. 1.4.2.1c). This area harbors deposits of a combined thickness of over 1 km. These deposits contain layers of volcanic tuffs, which are amenable to $^{39}\text{Ar}/^{40}\text{Ar}$ dating, and of clay, silt, sand, and carbonates (Fig. 1.4.2.1d).

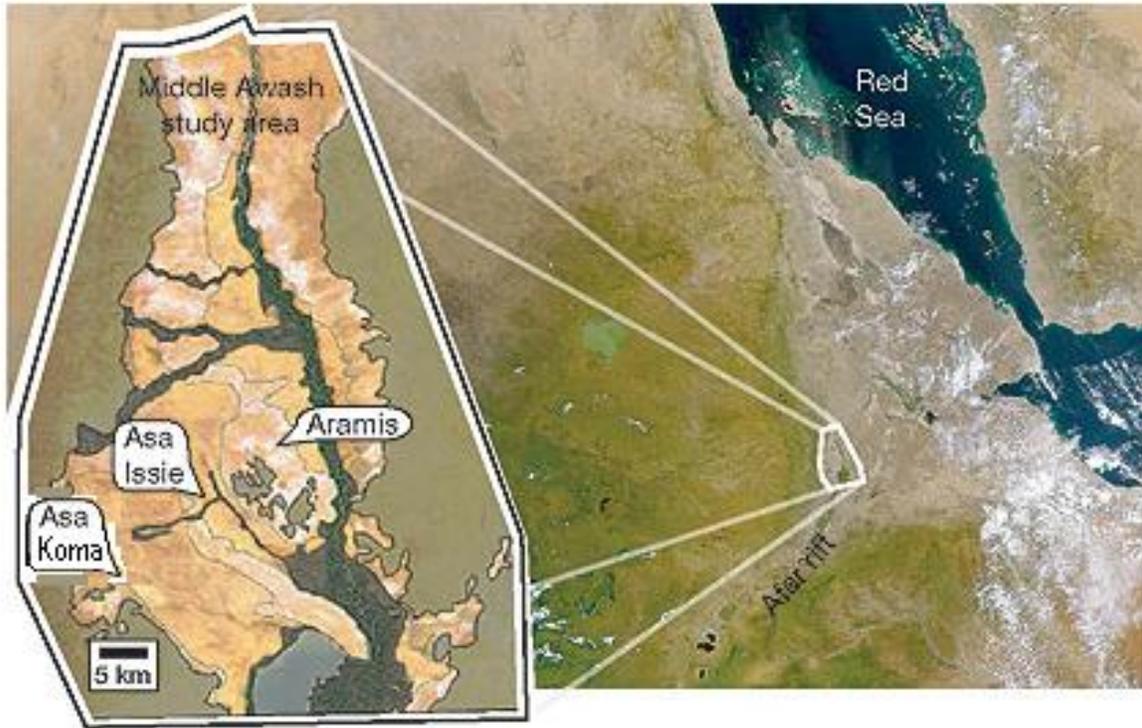


Fig. 1.4.2.1c. Middle Awash area of the Afar rift, with three of many sites of fossil discovery shown. 5.8 Ma fossils of *Ardipithecus kadabba* were found at the Asa Koma site; 4.4 Ma fossils of *Ardipithecus ramidus* were found at the Aramis site; and 4.2 - 4.1 Ma fossils of *Australopithecus anamensis* were found at Asa Issie site. Other hominin fossils found within the Middle Awash area include 3.4 Ma *Australopithecus afarensis* (Maka site), 2.5 Ma *Australopithecus garhi* (Bouri site), 1.0 Ma *Homo erectus* (Bouri site), 0.64 Ma archaic *Homo sapiens* (Bodo site), and 0.15 Ma *Homo sapiens* (Bouri site) (*Nature* 412, 175, 2001; *Nature* 440, 1100, 2006).

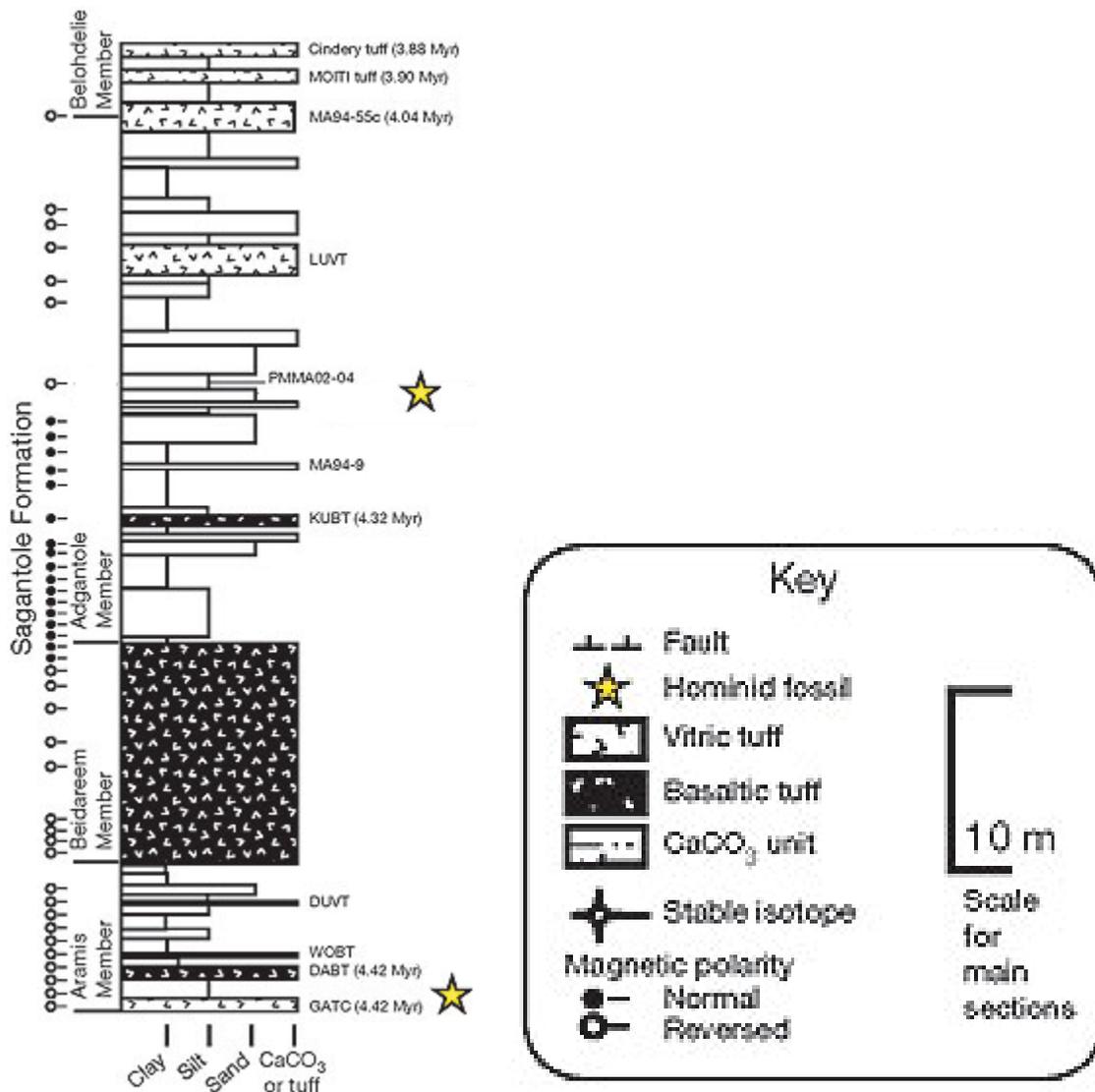


Fig. 1.4.2.1d. A segment of the stratigraphy (4.42 - 3.88 Ma) of the Middle Awash area, within which *Ar. ramidus* (bottom) and *Au. anamensis* (top) fossils reside.

Ardipithecus kadabba (kadabba = "family ancestor" in Afar) refers to a number of ~5.8 - 5.2 Ma fossils, so far represented only by teeth and fragments of skeletal bones. Apparently, these fossils are very similar to *Ar. tchadensis* and *Ar. tugenensis*, so that it may be more appropriate to place them all into the same species. Still, derived dental characters of *Ar. kadabba* are shared exclusively with younger hominids. Thus, *Ar. kadabba* probably belongs to the hominid clade. (Fig. 1.4.2.1e).

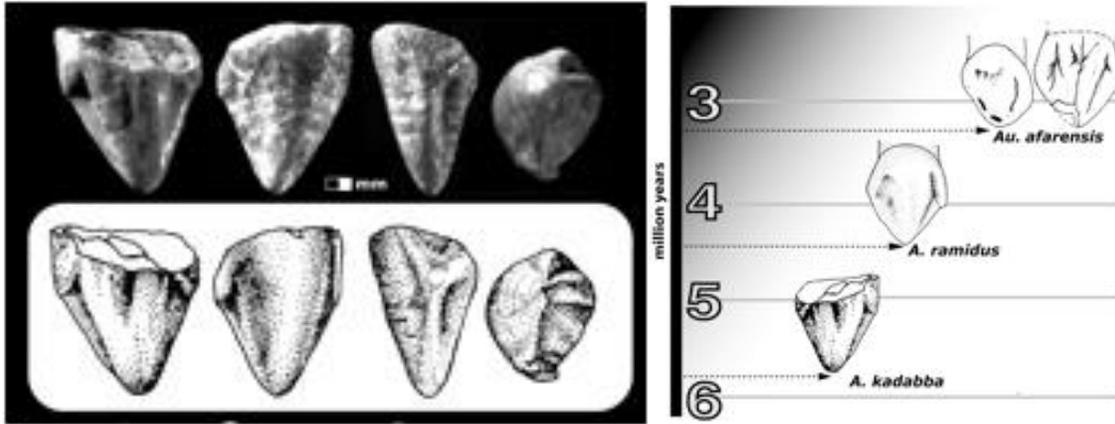


Fig. 1.4.2.1e. (left) Lingual, labial, mesial, and occlusal views of right upper canine tooth of *Ardipithecus kadabba*. (right) Trajectory of evolution of the canine teeth (lingual view) early in the human clade (*Science* 303, 1503, 2004).

Finally, 4.42 Ma we encounter much more complete hominin fossils. These fossils, known as *Ar. ramidus* ("ramid" = root in Afar), were mostly found between two tuff layers in Middle Awash area (Figs. 1.4.2.1d,f). These layers have the same, within the margin of error, age of 4.42 Ma, indicating that the interval between their depositions was below 100 Ka. Among *Ar. ramidus* fossils there is a partial skeleton, including most of the skull and teeth, as well as the pelvis, hands, and feet, which belong to a female that stood 120 cm and weighted ~50 kg (Fig. 1.4.2.1g), as well as various specimens from dozens of other individuals. These fossils revealed several important facts.

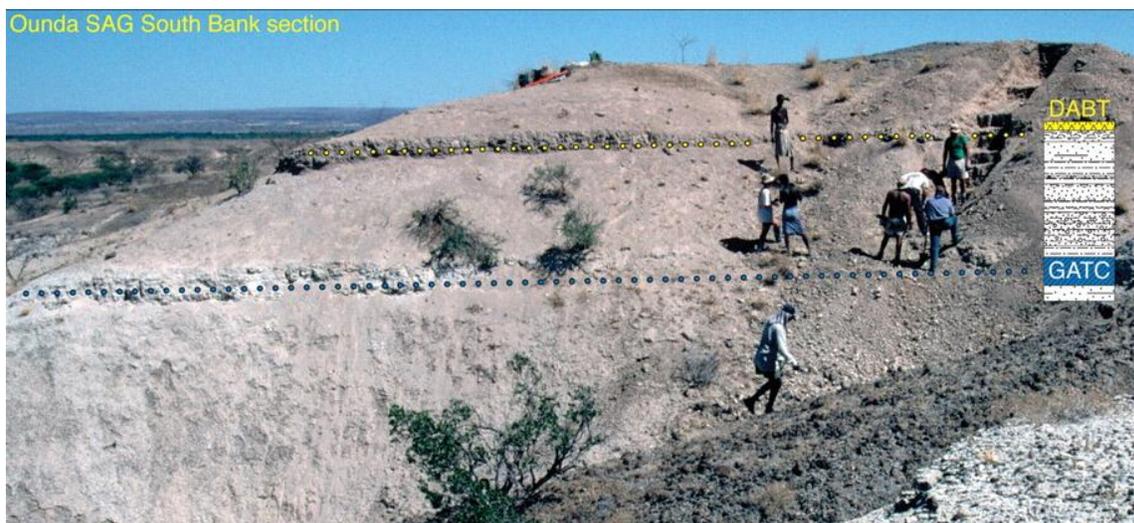


Fig. 1.4.2.1.f. The site where partial skeleton of *Ar. ramidus* was found, with its stratigraphic positions between two tuff layers, GATC and DABT (Fig. 1.4.2.1d) shown.

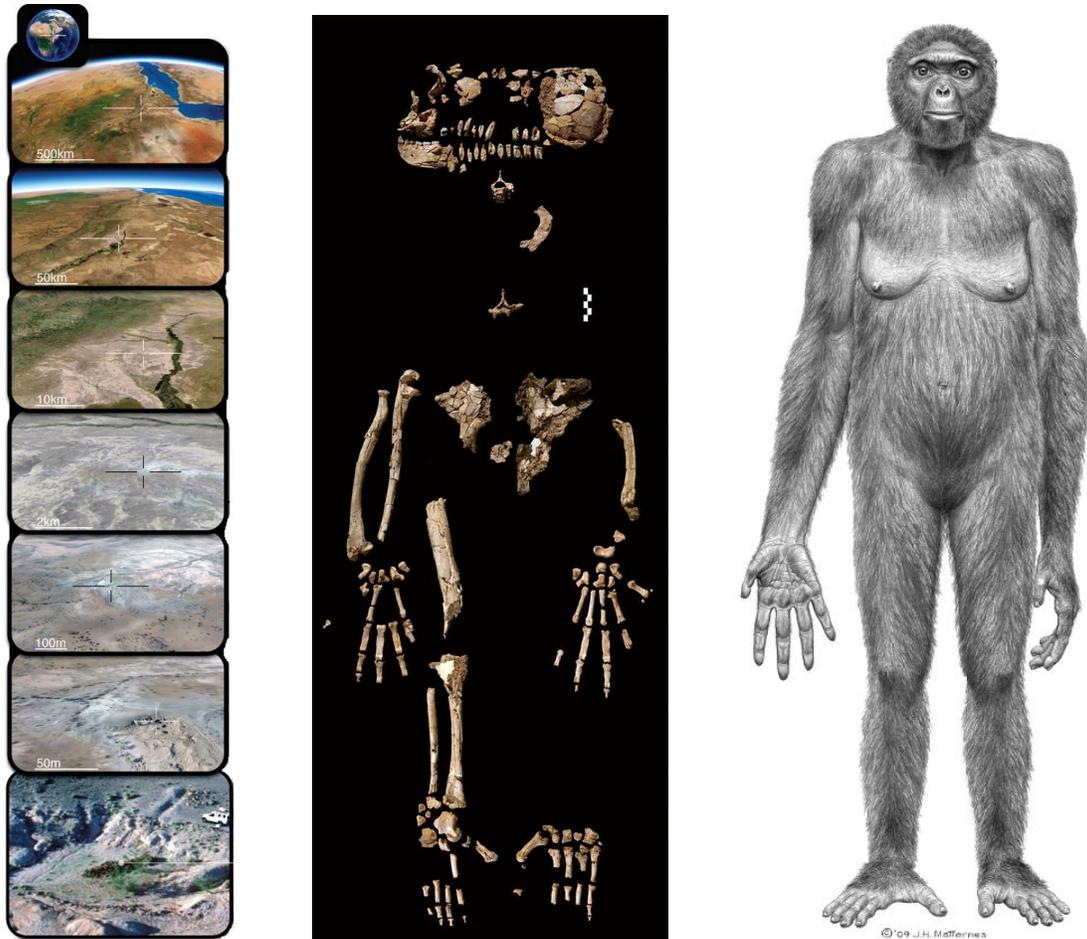


Fig. 1.4.2.1.g. The exact site of discovery, partial skeleton, and reconstruction of *Ardipithecus ramidus*.

The *Ar. ramidus* skull is rather similar to the skull of *Ar. tchadensis* and is substantially different from skulls of both extant apes and of the *Australopithecus* segment of the human clade (Section 1.4.2.2). Cranial capacity of *Ar. ramidus*, 300-350 cm³, is small, both absolutely and relatively to body size. *Ar. ramidus* lacked extreme prognathism (projecting jaws) of modern African great apes, which strongly suggests that the HCLCA lacked prognathism, and projecting jaws of gorillas and chimpanzees are the result of homoplasy. However, *Ar. ramidus* did have projecting midface.

Teeth of *Ar. ramidus* suggest omnivory, and lack several specialized adaptations found in extant great apes. Values of $\delta^{13}\text{C}$ obtained for the enamel of *Ar. ramidus* teeth suggest a diet consisting mostly of plants that use the C_3 photosynthetic pathway, with only a small C_4 component. Because C_4 photosynthesis is common in grasses and sedges of open habitats, this implies predominantly forest or woodland feeding. A variety of fossils of fruit-eating animals, as well as fossil wood, pollen, and seeds of trees, found together with *Ar. ramidus* tell the same story. Generally, teeth of *Ar. ramidus* are small, relative to body size. In particular, small canine teeth that apparently lacked sexual dimorphism, which suggest that within-species aggression was not common.

Postcranial bones of *Ar. ramidus* show that it was capable both to walk on the ground on two legs (bipedal terrestrial walking) and to move in the trees, supported on feet and palms (arboreal palmigrade clambering), because its feet were capable of grasping. In contrast, *Ar. ramidus* was likely incapable of vertical climbing or knuckle-walking, again suggesting that the state of a phenotypic trait which is common to gorillas and chimpanzees may be a result of homoplasy, and, thus, may be absent in the HCLCA.

Thus, it appears that HCLCA and the early stages of later evolution of the human clade were represented by small, non-specialized hominds, which had rather small brains, were both arboreal and bipedal (or, at least, evolved bipedality soon after the HCLCA), ate a variety of foods, and lacked many prominent adaptations of the extant great apes. Of course, more fossils from the crucial early period of human evolution are needed.

It also seems very likely that *Ardipithecus* simply represents the earliest segment of a single human lineage, whose next segment is referred to as *Australopithecus*, and which later led to modern humans, as well as to now-extinct *Paranthropus*, non-African *Homo erectus*, and *H. neanderthalensis* (Section 1.4.3). Indeed, ancestor-descendant relationships between *Ardipithecus* and *Australopithecus* are consistent with all the available data. In contrast, there is no evidence that *Ardipithecus* and *Australopithecus* ever lived simultaneously.

1.4.2.2. *Australopithecus*

The second segment of the human lineage known as *Australopithecus* (Southern Ape) covers the 4.3-2.5 Ma time interval. Its earliest part has been called *Au. anamensis*

("anam" = lake in Turkana). Fossils of *Au. anamensis* date to 4.2 - 3.9 mya and were found near the Lake Turkana in Kenya as well as at the Asa Issie site in the Middle Awash area (Fig. 1.4.2.1c). Thus, some *Au. anamensis* fossils are stratigraphically superimposed on *Ar. ramidus*, and the two are separated by ~80 vertical meters of deposits which represent ~300,000 years (Fig. 1.4.2.1d).

The fossils of *Au. anamensis* discovered so far include many fragments of the cranium, jaws, teeth, vertebra, and arm and leg bones. Still, they are less complete than the earlier fossils of *Ar. ramidus* or the later fossils of *Au. afarensis*. Nevertheless, it is clear that *Au. anamensis* was morphologically intermediate between *Ar. ramidus* and *Au. afarensis*, with variation that overlaps in both directions. Because only 300,000 years separate *Au. anamensis* from *Ar. ramidus*, evolution during this time must be relatively rapid.

In particular, teeth of *Au. anamensis* are substantially larger than that of *Ar. ramidus*, and more similar to the teeth of later *Au. afarensis* (Fig. 1.4.2.2a). Generally the masticatory apparatus of *Au. anamensis* appears better adapted to a more heavily chewed diet of tough and abrasive items than that of *Ar. ramidus*. The femurs of *Au. anamensis* and *Au. afarensis* are similar, and indicate more advanced mode of bipedal walking than in *Ar. ramidus*. Fossils of other vertebrates found with *Au. anamensis* in Middle Awash, as well as $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of palaeosols interbedded with these vertebrate fossils, demonstrate that *Au. anamensis* lived in a humid, grassy, woodland savannah environments, where 25–35% of grasses had C_4 photosynthesis.



Fig. 1.4.2.2a. Occlusal and lateral views of mandibles of *Ar. ramidus* (left, 4.4 Ma), *Au. anamensis* (center, 4.12 Ma), and *Au. afarensis* (right, 3.4 Ma) (*Science* 326, 75, 2009).

The mixture of ancestral and derived trait states shows that *Au. anamensis* to be a very likely ancestor to the next species recognized within the *Australopithecus* segment of the human clade, *Au. afarensis*. *Au. afarensis* fossils span the range of 3.8 - 3.0 Ma and are known from Maka site in the Middle Awash area (Fig. 1.4.2.1c), Hadar (also in the valley of the Awash river), and several other localities in Ethiopia, Kenya, Tanzania, and Chad. They include a famous 3.2 Ma partial female skeleton discovered in 1974 and named Lucy (Fig. 1.4.2.2b), a well-preserved 3.3 Ma skeleton and skull of a 3-year old individual from Dikika area (also within the Awash valley), named Selam (Fig. 1.4.2.2c), teeth and bones from at least 13 individuals that apparently died together, collectively known as "First Family", and many others. Also, a valuable trace fossil which almost certainly belong to *Au. afarensis* is known. This fossil is 3.75 Ma footprints, left in a layer of hardened volcanic ash, discovered in Laetoli, Tanzania. Their age was easy to determine, because the ash can be dated using $^{39}\text{Ar}/^{40}\text{Ar}$ analysis. Probably, two *Australopithecus afarensis* individuals left the footprints as they walked across the savanna after a big eruption (Fig. 1.4.2.2d).

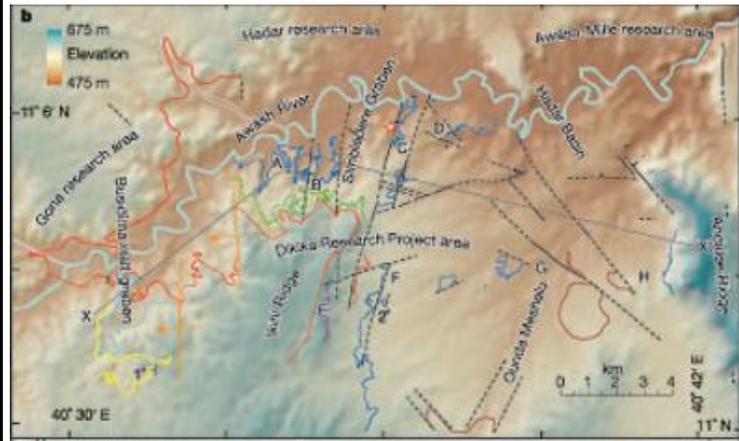


Fig. 1.4.2.2b. Lucy, a partial skeleton of *Au. afarensis* from Hadar (left) and Hadar and Dikika areas (right).



Fig. 1.4.2.2c. Selam, a skull and partial skeleton of *Au. afarensis* from Dikika. (left) anterior, lateral, and posterior views of the skull; (center) arm and leg bones; (right) dentition, hyoid bone, and manual phalanges (*Nature* 443, 296, 2006).



Fig. 1.4.2.2d. Laetoli footprints, almost certainly left by two *Au. afarensis* individuals (left) and their reconstruction (right).

This extensive fossil record made it possible to establish a number of key facts about *Au. afarensis*, although many other features of this species remain uncertain. Lucy stood ~ 1.3 m tall, and *Au. afarensis* males were larger, but we do not know by how much. Estimates of *Au. afarensis* sexual dimorphism range from moderate, observed in modern humans, to extensive, observed in gorillas. Clearly, a male skeleton would be very valuable.

Cranial capacity of *Au. afarensis* was 400 - 450 cm³, *i. e.*, was slightly larger than that of *Ar. ramidus*. *Au. afarensis* had more projecting jaws than *Ar. ramidus*, and its craniofacial features, including relatively large molars with thick enamel, are likely adaptations to heavy chewing. Hyoid (lingual) bone of *Au. afarensis* is similar to that of chimpanzees and gorillas, and different from that of *Homo*; thus, *Au. afarensis* almost certainly was incapable of articulated speech. Upper body of *Au. afarensis* is still

essentially ape-like. In contrast, its lower body is much more derived and adapted for bipedal locomotion. In contrast to *Ar. ramidus*, the foot of *Au. afarensis* was not capable of grasping, so that bipedal terrestrial walking was the main form of its locomotion. However, it is not clear whether *Au. afarensis* also spent a substantial part of its time on trees, as its gorilla-like scapula (shoulder bone) and long and curved manual phalanges may suggest. Fossils found with *Au. afarensis*, including many species of mammals, freshwater gastropods, fishes, and pollen, suggest that it inhabited a wide variety of environments, including mostly wooded areas, open grasslands, and river banks.

The later portion of the *Australopithecus* segment of the human lineage is known from 3.0 - 2.5 Ma fossils found at four sites in South Africa, referred to as *Au. africanus*. In fact, ages of *Au. africanus* fossils have been established only indirectly, because most of them were found in caves. Cranium, jaws, and teeth of *Au. africanus* are well-represented (Fig. 1.4.2.2e), but postcranial fossils are rather incomplete. *Au. africanus* was similar to *Au. afarensis*, but its body and cranial capacity of $\sim 460 \text{ cm}^3$ were slightly larger and facial features were more humanoid. The shape of the jaw is now fully parabolic, like that of humans, and the size of the canine teeth is reduced compared to *Au. afarensis*. Still, it had relatively large chewing teeth and apart from the reduced canines the skull is relatively ape-like. Data on $\delta^{13}\text{C}$ indicate that *Au. africanus* ate not only fruits and leaves but also large quantities of ^{13}C -enriched foods such as grasses and sedges with C_4 photosynthesis and/or animals that fed on such plants, suggesting that *Au. africanus* exploited open habitats.

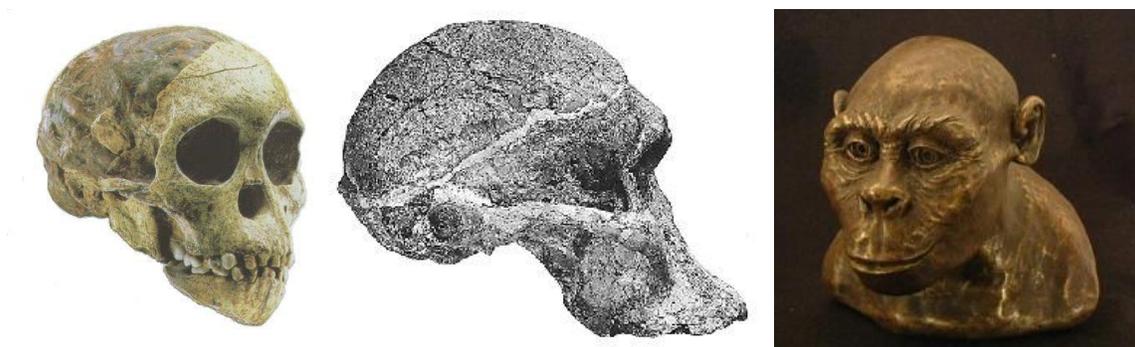


Fig. 1.4.2.2e. *Au. africanus*: fossils found in South Africa, Taung child (left) and Mrs. Ples (center), and reconstruction (right).

1.4.2.3. *Homo*

The third and final segment of the human lineage, referred to as *Homo*, spans the time from 2.4 Ma until present. Fossils with cranial capacity 500 - 750 cm³, substantially above that of *Australopithecus*, and smaller teeth are known starting from 2.4 Ma at several East African localities, including Olduvai Gorge in Tanzania and Koobi Fora Formation in Kenya. These fossils represent mostly cranial and dental remains and only a few postcranial bones (Fig. 1.4.2.3a), and are attributed to one species, *Homo habilis*.

H. habilis was still similar to *Australopithecus* in many ways. The face of *H. habilis* remained primitive, although it projected less than in *A. africanus*. The back teeth are smaller than in *A. africanus*, but still larger than in modern humans. Like *Australopithecus*, *H. habilis* stood ~1.3 m, weighted 30-40 kg and had similar limb proportions, in particular, long arms.

Still, the brain shape in *H. habilis* was more humanlike than in *Australopithecus*. The bulge of Broca's area, essential for speech, is visible in the brain cast of one *H. habilis*, indicating that it was capable of rudimentary speech. Also, *H. habilis* was likely the first regular maker of stone tools.



Fig. 1.4.2.3a. *Homo habilis* 1.8 Ma skull OH 24 (Twiggy) from Olduvai Gorge (left) and reconstruction (right).

Oldowan tools, discovered in the Olduvai Gorge, are the oldest kind of stone tools, consisting of cores and flakes, which were obtained by striking the cores on the edge with another stone (Fig. 1.4.2.3b). The oldest known Oldowan tools are from the Hadar area (Fig. 1.4.2.2b) and are ~2.6 Ma, raising the possibility that their maker was late *Australopithecus* (or even early *Paranthropus*, Section 1.4.3.1). However, most of known Oldowan tools were probably made by *H. habilis*. This tradition of making simple flakes struck off unmodified cores persisted until ~0.5 mya, alongside more sophisticated tools.



Fig. 1.4.2.3b. Oldowan tools.

Fossil which are more similar to modern humans appear from ~1.8 Ma and are attributed to *H. erects* (and sometimes to several other species). These fossils include a number of crania (Fig. 1.4.2.2c) and one nearly-complete skeleton (Turkana boy; Fig. 1.4.2.3d). *H. erects* had a long low skull with cranial capacity between 750 cm³ and 1225 cm³, with the averages being ~900 cm³ for early specimens and ~1100 cm³ for late specimens. Like *H. habilis*, *H. erects* had face with protruding jaws with large molars, no chin, thick brow ridges. The skeleton of *H. erectus* is more robust than those of modern humans. Body proportions vary; the Turkana Boy is tall and slender. *H. erectus* may be a direct descendant of *H. habilis*. Some data seem to indicate that *H. habilis* and *H. erectus* coexisted 1.4 Ma, which would imply that only one of them could belong to the lineage of modern humans (*Nature* 448, 688, 2007). However, the evidence for this are inconclusive (*Annual Review of Earth and Planetary Sciences* 37, 67, 2009), and it would

be premature to abandon a simple hypothesis that there always was only one lineage of *Homo* in Africa.

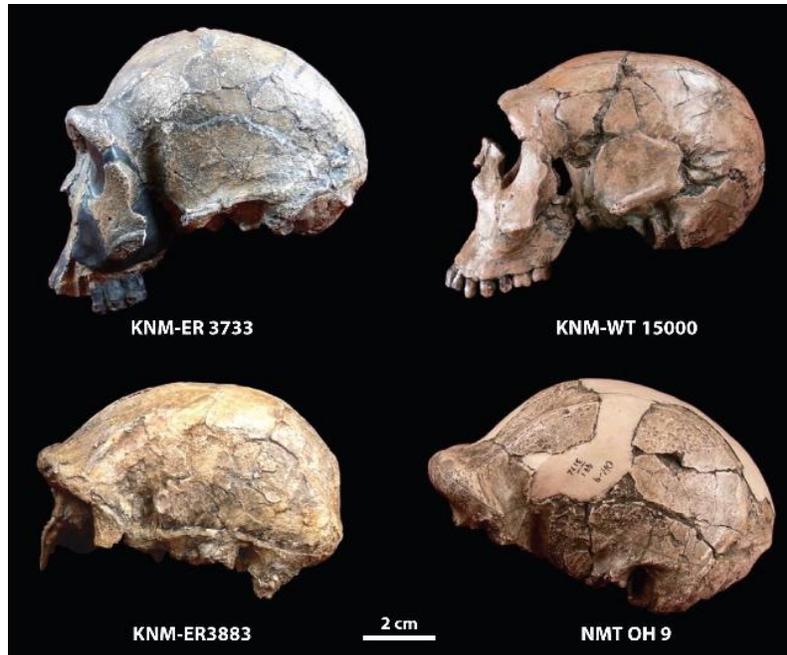


Fig 1.4.2.2c. Four skulls of *H. erectus* from East Africa. (*Annual Review of Earth and Planetary Sciences* 37, 67, 2009).



Fig. 1.4.2.3d. Turkana boy, 1.6 Ma skeleton of an 11-12 year old *H. erectus* boy, found near Lake Turkana in Kenya. The brain size was 880 cm³ (~910 cm³ at adulthood). A modern human of comparable size would be expected to have a brain size ~1350 cm³. The boy was 160 cm tall, and he might have been ~185 cm as an adult. Except for the skull, the skeleton is quite similar to that of modern boys.

Footprints discovered in two 1.53 and 1.51 Ma sedimentary layers at Ileret, Kenya (Fig. 1.4.2.2e) were likely left by *H. erectus*. These footprints are distinct from the 3.75 Ma Laetoli footprints (Fig. 1.4.2.2d) and show that by 1.5 Ma *H. erectus* had evolved an essentially modern human foot function and style of bipedal locomotion. A pelvis of adult *H. erectus* female that lived of 1.4 - 0.9 Ma is obstetrically capacious and demonstrates that pelvic shape in *H. erectus* was evolving in response to increasing fetal brain size (Fig 1.4.2.2f).

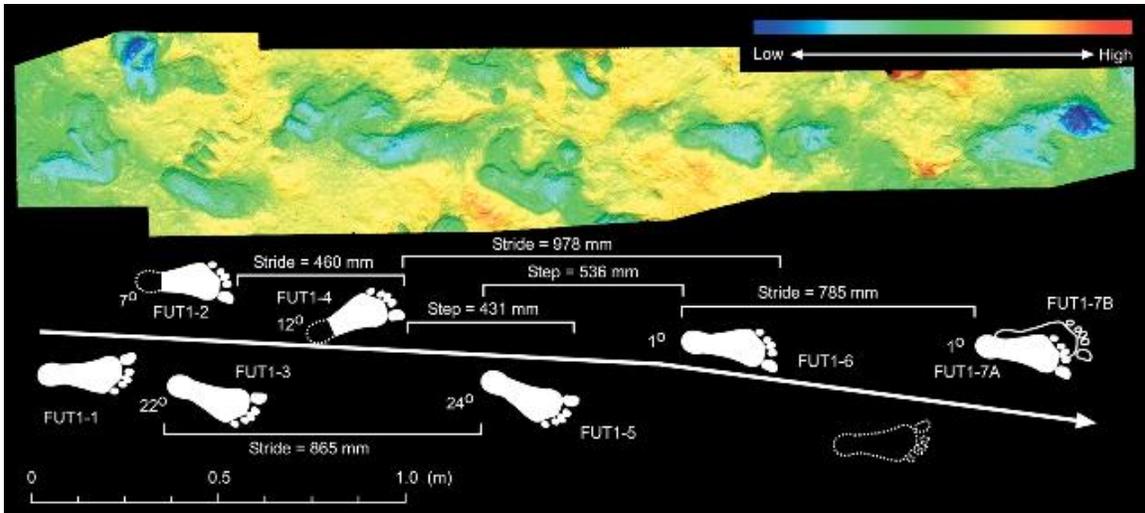


Fig. 1.4.2.2e. 1.5 Ma footprints from Ileret, Kenya, likely left by *H. erectus*.

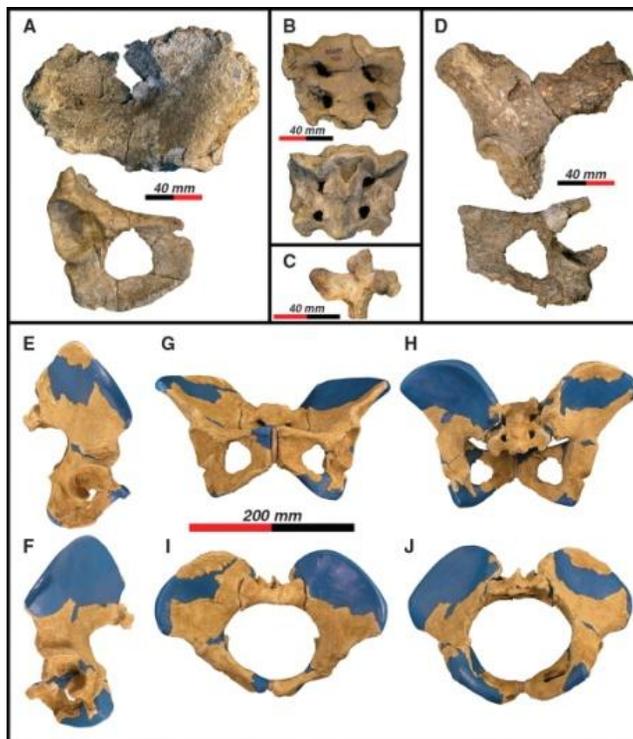


Fig. 1.4.2.2e. Pelvis of an 1.4 - 0.9 Ma *H. erectus* female (*Science* 322, 1089, 2008).

H. erectus made stone tools that are more sophisticated than those of *H. habilis* and apparently used fire. Acheulean tradition of stone tool-making, which replaced the more primitive Oldowan tradition, existed from 1.5 to ~0.2 Ma. Acheulean tools, likely

made and used by *H. erectus*, have been found in many of locations (Fig. 1.4.2.2f). The hand-axe that was the main feature of the Acheulean tradition has been described as the Swiss Army knife of prehistoric man, because it seems to be a multi-purpose instrument, suited to slicing, dicing, chopping, rooting and killing animals.



Fig. 1.4.2.2f. Acheulean hand-axes. Several *H. erectus* fossils were found together with Acheulean hand-axes, including one small ~0.9 Ma cranium, indicative of wide population variation in the hominins of this period (*Science* 305, 75, 2004).

It may be convenient to extend the temporal range of on *H. erectus* until ~0.6 Ma. However, the human lineage changed substantially between 1.8 and 0.6 Ma. For example, 1.0 Ma calvaria and postcranial remains of a *H. erectus* (Daka) are anatomically intermediate between earlier and later African fossils. Its endocranial capacity is relatively high at 995 cm³, but brow ridges are thick and strongly arched. Daka hominid was found in sediments containing abundant early Acheulean stone tools and a diverse vertebrate fauna that indicates a savannah environment. Its temporal and geographic position indicates that African *H. erectus* was the ancestor of *H. sapiens*.



Fig. 1.4.2.2g. Daka calvaria (top of the skull) which belongs to a 1.0 Ma *H. erectus* found at the Bouri site in Middle Awash (*Nature* 416, 317, 2002).

Anatomically modern humans evolved gradually (of course!) from *H. erectus* in Africa. Several transitional fossils are known, but not very many. The boundary between *H. erectus* and *H. sapiens* can be put at 600 Ka, because it is probably unnatural to regard the ~600 Ka cranium from the Bodo site in Middle Awash (Fig. 1.4.2.2h) as *H. erectus*. This cranium possesses a mixture of ancestral and derived trait states, but, crucially, its endocranial capacity was 1300 cm³, which is close to that of modern humans.

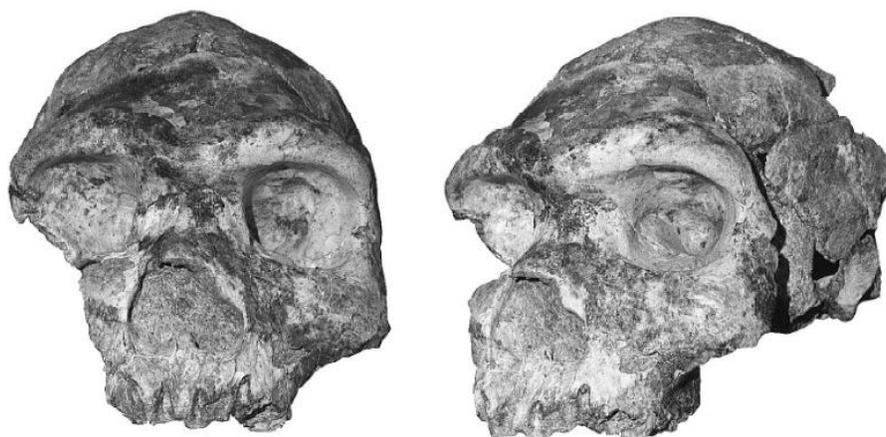


Fig. 1.4.2.2h. Archaic *H. sapiens* from the Bodo site in Middle Awash (*J. Hum. Evol.* 31, 21, 1996).

Fossils of two adult and one immature human were discovered in the Herto Member, at the Bouri site in Middle Awash (Fig. 1.4.2.2i). These 160 -154 Ka fossils are

morphologically and chronologically intermediate between archaic African fossils and later anatomically modern humans, are associated with both Acheulean and Middle Stone Age tools, and probably represent the immediate ancestors of anatomically modern humans. Indeed, the morphology of the Herto crania falls between the more primitive morphology of the earlier African specimens, such as Bodo and Kabwe, and the more derived morphology of later anatomically modern *H. sapiens*, such as Qafzeh (Fig. 1.4.2.2j). There is no evidence of cladogenesis during the evolution of *H. sapiens* from *H. erectus* in Africa. Among the global sample of modern humans, the Herto crania lack any derived affinity with modern African crania or with any other group, which is to be expected for a common ancestor.

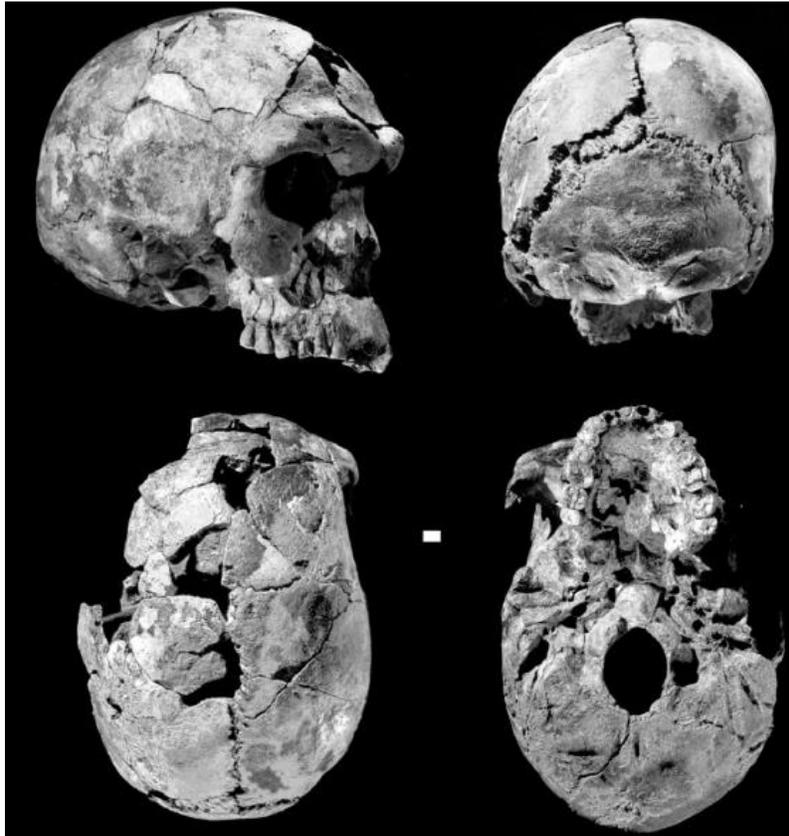


Fig. 1.4.2.2i. Cranium of an adult *H. sapiens* from Herto (Nature 423, 742, 2003).

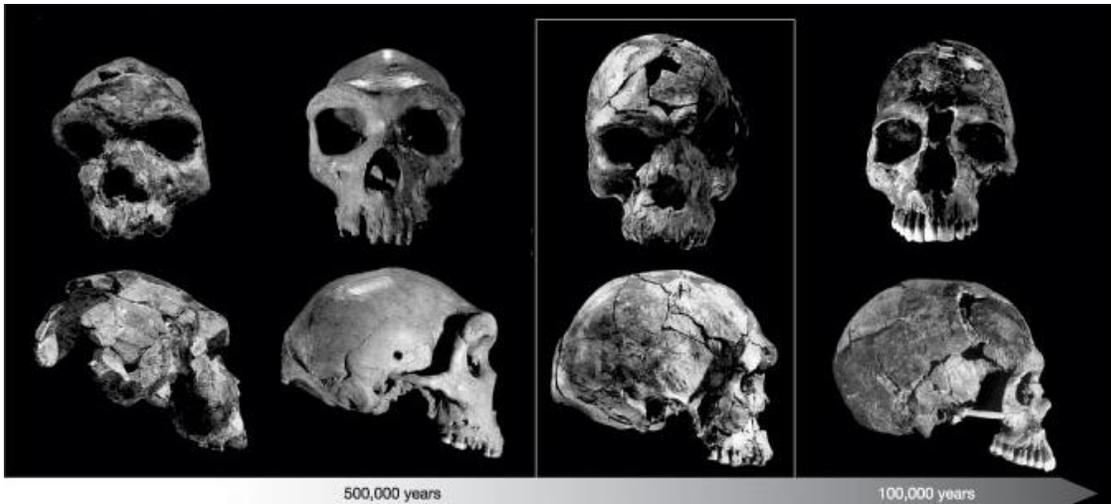


Fig. 1.4.2.2j. Comparison of crania with earlier and later fossils. From left to right, in anterior and lateral views, Bodo, Kabwe, Herto (boxed), and Qafzeh crania, with approximate time line.

1.4.2.4. Origin of modern human diversity

Data on genetic variation within modern humans show that ancestors of all modern humans lived in Africa until ~100-70 kya, after which some of them dispersed across the globe, reaching Australia ~30 kya and Americas ~15 kya (Fig. 1.4.2.4a, b). Indeed, all alleles present at a locus among modern humans can be traced to the common ancestral allele 100-400 Kya, and alleles found in non-African modern humans represent only one clade on the genealogy (phylogeny) of all human alleles (Fig. 1.1.3.7g). The numbers of individuals that established new populations in the course of the global expansion of humans were often not large, leading to decline of genetic variation within populations that are further away from Africa.

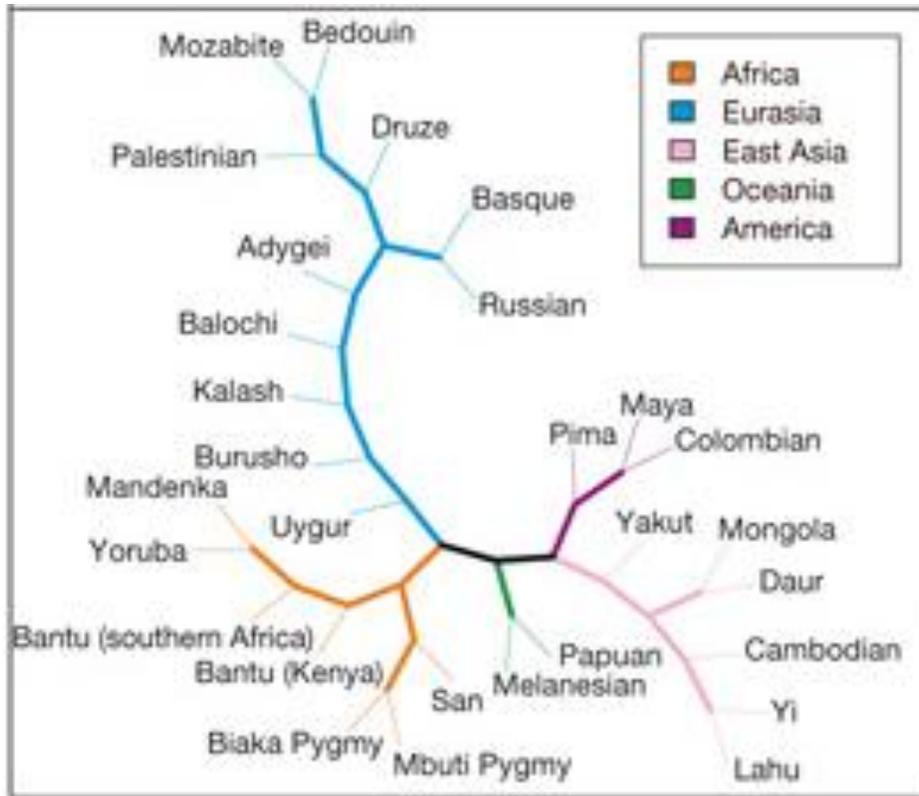


Fig. 1.4.2.4a. Pattern of genetic similarity between modern human populations, from which the history of recent human dispersal has been inferred (*Nature* 451, 998, 2008).

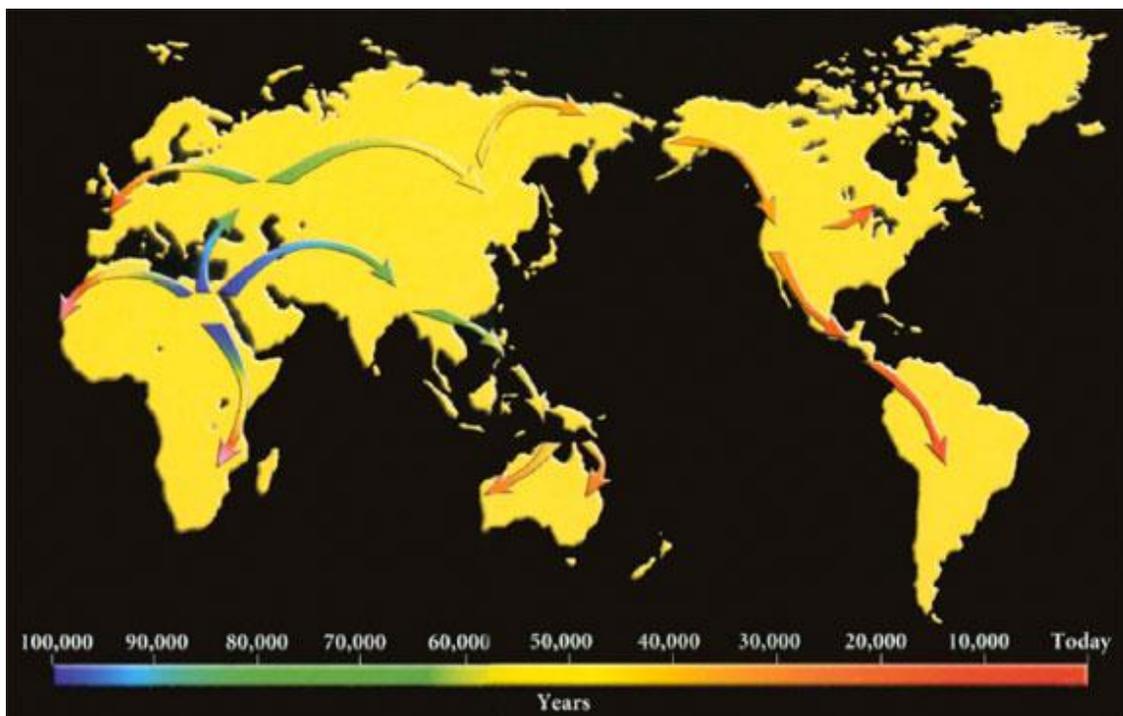


Fig. 1.4.2.4b. The scheme of dispersal of *H. sapiens* from Eastern Africa.

1.4.2.5. Factors of human evolution

Even the factors responsible for morphological changes in the human lineage are not entirely clear. We do not know for sure why our ancestors choose bipedality as their mode of terrestrial locomotion, instead of knuckle-walking or some other solution. Increased size of jaws and molar teeth in *Australopithecus* was probably due to consumption of rough foods, and the reversal of this trend in *Homo* may be plausibly explained by usage of tools and, later, fire for processing foods, but this is not definite. Indeed, fossils do not tell us what factors lead to natural selection which shaped their phenotypes.

The factors responsible for the evolution of human cognitive abilities are even more mysterious. Clearly, there could be no direct selection on human ability to enjoy sophisticated music or to prove advanced mathematical theorems, because sophisticated music and mathematics did not exist until very recently. One can say that such abilities evolved as by-products of natural selection for other cognitive functions, but this does not explain much. Human linguistic abilities also seem to exceed by far what was needed for hunters-gatherers in their daily activities, although here social interactions may be the key factor. The genetic basis of the corresponding changes is also currently obscure: we do not know how many allele replacements it would take to make a chimpanzee capable of proving the Fermat's Last Theorem (Fig. 1.4.2.5a). This subject is discussed in Part 4.

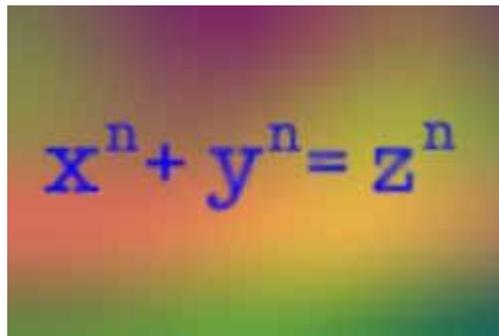
The image shows the mathematical equation $x^n + y^n = z^n$ written in a blue, serif font. The equation is centered on a rectangular background with a vertical color gradient from purple at the top to green at the bottom.

Fig. 1.4.2.5a. Fermat's Last Theorem states that this equation does not have a solution in integer numbers when $n > 2$.

Although different populations of modern humans mostly harbor the same alleles (Chapter 2.2), these populations are profoundly different from each other in some important traits. Clearly, natural selection must play the key role in rapid origin of differences between tightly related populations. For traits such as sickle-cell anemia or ability of adults to digest milk the corresponding selective forces are clear, but this is not the case for other conspicuous traits such as skin color or body size.

Section 1.4.3. Our extinct close relatives

In addition to the lineage which eventually led to modern humans, the human clade after the HCLCA comprises at least three smaller clades which are now extinct and are thus known only from fossils. The first side clade branched off the human lineage ~2.5 mya and was represented by bipedal hominins with robust skulls, attributed genus *Paranthropus*, which went extinct ~ 1.4 mya. The second side clade appeared as a result of the first out-of-Africa expansion of the human lineage ~2.0 mya, and is represented by non-African *Homo erectus*, which produced a variety of forms throughout Eurasia and Indonesia, the last of which went extinct only 12 kya. The third side clade is represented by the Neanderthals *Homo neanderthalensis*, which were likely produced through the second out-of-Africa expansion of the human lineage ~0.5 mya, lived mostly in Europe and went extinct ~30 kya.

1.4.3.1. Paranthropus

Between 2.5 and 1.4 Ma, bipedal hominins with robust skulls and very large teeth (megadent), in particular molars, lived in Africa. These hominins are usually referred to as several species of genus *Paranthropus* ("besides human"). They probably represent a single clade, although this is not certain. The exact timing of cladogenesis (or cladogeneses) that produced robust hominins remains unknown, but it very likely occurred after 3.0 Ma, and *Au. afarensis* is almost certainly the common ancestor, although not necessarily the last one, of *Homo* and *Paranthropus*. A 2.5 Ma fossil from the Bouri site of the Middle Awash, originally described as *Au. garhi*, may be at the base

of the *Paranthropus* clade, in which case it would be better to call it *P. garhi* (Fig. 1.4.3.1a).

Robust hominins are attributed to species *P. aethiopicus*, *P. robustus*, and *P. boisei*, although it is not clear whether different robust hominins that were reproductively isolated from each other ever coexisted. All of them had cranial capacity of $\sim 550 \text{ cm}^3$. Their faces were flat or dish-shaped, with no forehead and large brow ridges. Front teeth were relatively small, but grinding teeth were massive, with some molars being up to 2 cm across, and a lower jaw was large. Paranthropuses were fully bipedal, stood 1.3 - 1.4 m, with body mass 40-50 kg, had thick bones and robust muscles, and were adapted to very rough plant diet.



Fig. 1.4.3.1a. *Au. garhi*, a possible basal member of the robust megadent clade of hominins (*Journal of Anatomy* 212, 354, 2008).



Fig. 1.4.3.1b. (left) *P. boisei* skull, discovered in Olduvai Gorge in Tanzania. (center) *P. boisei* lower jaw. (right) Reconstruction of paranthropuses.

1.4.3.2. Non-African *Homo erectus*

After 1.8 Ma, many *H. erectus* populations became the first hominins to become established outside Africa, in Southern Eurasia and Indonesia (Fig. 1.4.3.2a). Later, these populations underwent substantial evolution. However, there are no traces of contribution of these populations into the gene pool of modern humans and, instead, the last of them went extinct ~12,000 years ago.



Fig. 1.4.3.2a. The known range and sites of important fossil discoveries of *H. erectus*, within and outside of Africa.

Early non-African *H. erectus* fossils include a 1.8 ± 0.04 Ma cranium found in Mojokerto, Java (*Nature* 438, 1099-1104, 2005). A number of important fossils come from Dmanisi in Georgian Caucasus, where bones and artifacts were deposited during a brief interval ~ 1.77 Ma (Fig. 1.4.3.2b). The crania found there have capacities of 600 - 775 cm³, and resembles *Homo habilis* in brain volume and some aspects of craniofacial morphology. Still, other characters and measurements suggest that the Dmanisi skulls are best placed within *H. erectus*. The postcranial anatomy of the Dmanisi hominins is also a mosaic of ancestral and derived features. The ancestral features include a small body size, a low encephalization quotient and absence of humeral torsion; the derived features include modern-human-like body proportions and lower limb morphology indicative of

the capability for long-distance travel (*J. of Hum. Evol.* 50, 115-141, 2006; *Nature* 434, 717-718, 2005; *Nature* 449, 305-310, 2007).

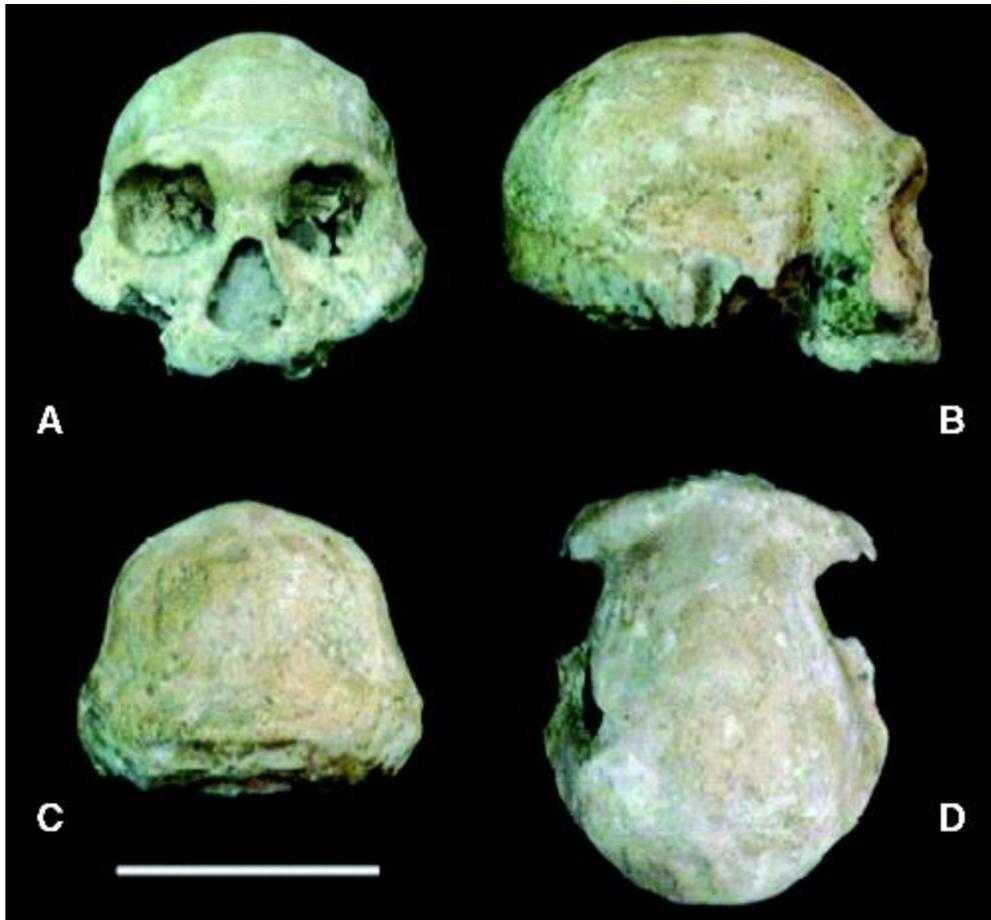


Fig. 1.4.3.2b. The D3444 *H. erectus* cranium from Dmanisi. Scale bar = 10 cm (*Anatomical Record* 288A, 1146, 2006).

The earliest known hominid from Europe is only ~1.2 Ma (*Nature* 452, 465, 2008). *H. erectus* populations lived in Eurasia until at least 680 Ka (Fig. 1.4.3.2c), and probably even much later. The population of *H. erectus* from the Zhoukoudian cave system near Beijing, China (Peking man) lived there between 780 and 680 Ka, and had cranial capacities between 1000 and 1225 cm³. Thus, increased brain size evolved in parallel, and probably independently, in the human ancestral lineage within Africa and in *H. erectus* outside Africa, although genetic exchanges between them cannot be ruled out. The population of *H. erectus* from Java, known from 1.8 Ma, survived until 30-50 Ka,

and very likely overlapped with modern humans (*Science* 274, 1870, 1996; *Science* 299, 1384, 2003).



Fig. 1.4.3.2c. *H. erectus* skull from Zhoukoudian (*Nature* 458, 198, 2009).

On the Island Flores, Indonesia, there lived, until ~12 Ka, a hominid with adults being only ~1 meter tall and having cranial capacity of only ~420 cm³ (Fig. 1.4.3.2d). This hominin almost certainly evolved from non-African *H. erectus*, but is commonly referred to a distinct species, *H. floresiensis*. Indeed, reduced body size often evolves in isolated island populations (Chapter 1.5). Notwithstanding its small brain, the behavior of *H. floresiensis* was probably advanced. Their cave shows evidence of the use of fire for cooking, they have been associated with stone tools of the sophisticated Upper Paleolithic tradition, and *Stegodon* (an elephant relative) bones associated with *H. floresiensis* have cut marks. Some of these tools were apparently used in the necessarily cooperative hunting of *Stegodon* by these hominins.



Fig. 1.4.3.2d. *H. floresiensis*: range, skull, thigh bones, and reconstruction (*Nature* 431, 1055, 2004; *Journal of Human Evolution* 57, 538, 2009).

1.4.3.3. *Homo neanderthalensis*

Our sister clade, *H. neanderthalensis*, is known from fossils between 230 and 28 Ka. The average brain size of the Neanderthals was $\sim 1450 \text{ cm}^3$, slightly larger than in modern humans. The brain case is longer and lower than that of modern humans, with a marked bulge at the back of the skull. Like *H. erectus*, Neanderthals had a protruding jaw and receding forehead. The chin was usually weak. The midfacial area also protrudes, a

feature that is not found in *H. erectus* or *H. sapiens* and may be an adaptation to cold (Fig. 1.4.3.3a). There are other minor anatomical differences from modern humans, including some peculiarities of the shoulder blade, and of the pubic bone in the pelvis.



Fig. 1.4.3.3a. Neanderthal (left) and modern human (right) cranial differences (*Proc. Natl. Acad. Sci. USA* 106, 16022, 2009).

Neanderthals mostly lived in cold climates, and their body proportions are similar to those of modern cold-adapted peoples: short and solid, with short limbs. Men averaged about 168 cm in height (Fig. 1.4.3.3b). Their bones are thick and heavy, and show signs of powerful muscle attachments. A large number of tools and weapons have been found, more advanced than those of *Homo erectus*. Neanderthals were formidable hunters, and are the first people known to have buried their dead, with the oldest known burial site being about 100,000 years old. The Neanderthals survived in isolated refuges well after the arrival of modern humans in Europe (*Nature* 443, 850, 2006).

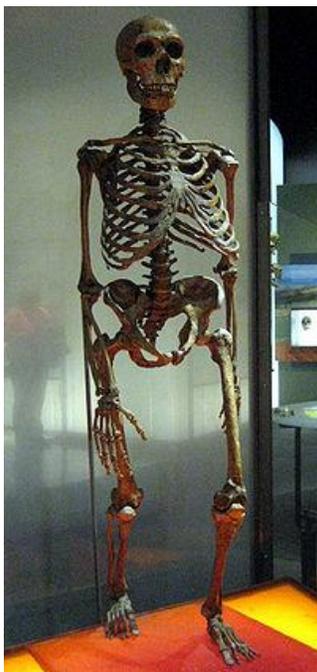
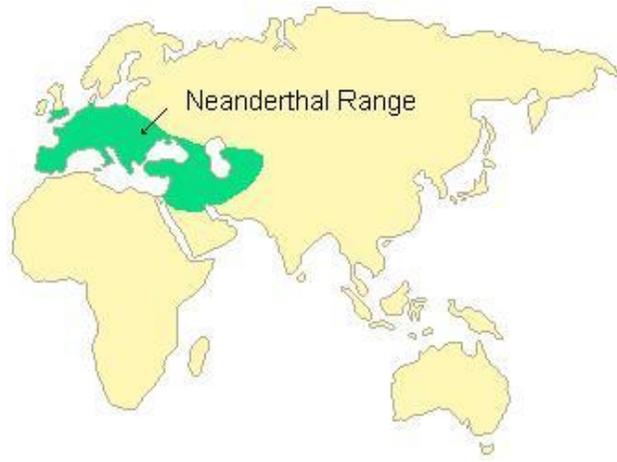


Fig. 1.4.3.3b. Neanderthals: Range, skeleton, a bone for which DNA has been taken for sequencing, and reconstructions.

Some Neanderthal bones contain fragments of DNA that are long enough for sequencing, and the first draft of a 38 Ka Neanderthal genome is already available. Comparison of Neanderthal, human, and chimpanzee genes reveals that modern human and Neanderthal DNA sequences diverged ~500,000 years ago (Fig. 1.4.3.3c). Thus, the origin of Neanderthals must involve yet another dispersal of humans from Africa, which occurred after the dispersal 1.8 Ma that produced non-African *H. erectus* but before the dispersal ~ 80 Ka which produced non-African *H. sapiens* (*Anthr. Sci.* 115, 133-151, 2007). There is no evidence of any contribution of Neanderthals, as well as of out-of-Africa *H. erectus* populations, into the gene pool of modern humans.

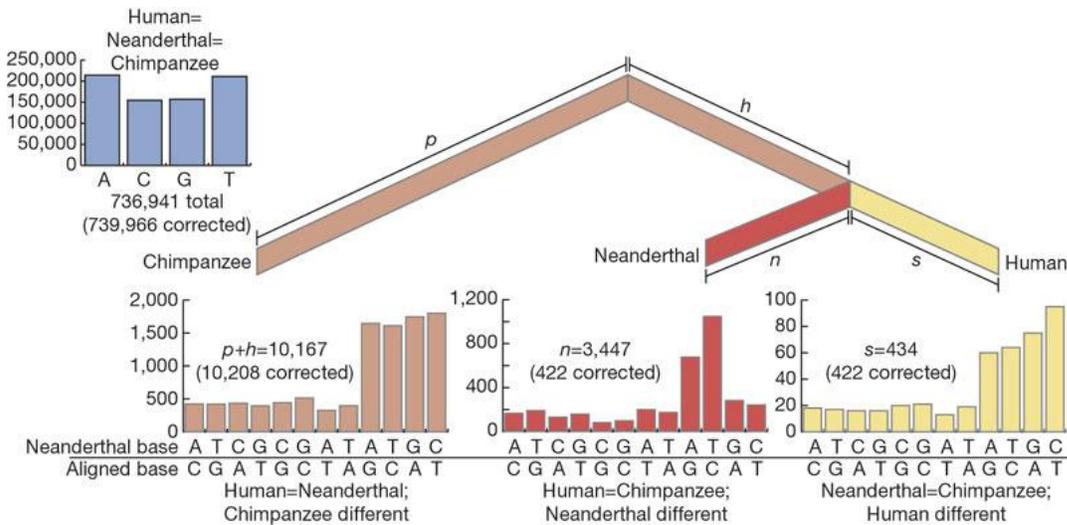


Fig.

1.4.3.3c. Dissimilarity of DNA sequences between *H. sapiens* and *H. neanderthalensis* is ~12 smaller than the dissimilarity of any of them and Pan troglodytes, implying that the last common ancestor of us and Neanderthals lived less than ~0.5Mya (the tree is not drawn to scale). In blue is the distribution of all aligned positions that did not change on any lineage. In brown are the changes that occurred either in the chimpanzee lineage (p) or in the hominin lineage (h) before the *H. sapiens* and *H. neanderthalensis* lineages diverged. In red are the changes that are unique to the Neanderthal lineage (n). In yellow are changes unique to the Sapiens lineage (s). The numbers of changes in each category, corrected for base-calling errors in the Neanderthal sequence, are shown within parentheses. (*Nature* 444, 330-336, 2006).

History and perspectives

In Darwin's time, there were almost no direct data on the evolutionary origin of humans. The discovery of Neanderthals, made in 1829, was announced only in 1857, but it became evident only much later that Neanderthals are not our ancestors. Key fossils of *Australopithecus africanus*, *Au. afarensis* and *Ardipithecus ramidus* has been discovered in 1924, 1974, and 1994, respectively. *Homo erectus* Turkana boy was found in 1984 and *H. floresiensis* in 2004. Important hominin fossils continue to be discovered, and modern methods of analysis play a major role in their interpretation. Recent history of our lineage is revealed mostly by the analysis of data on modern human diversity, and these data keep accumulating rapidly.

Perspectives. There are still many hominid fossils in the ground, and hopefully some of them will be discovered and described, shedding new light on the human origin. The topology of the phylogenetic tree of the human clade, and the nature of changes in the course of its evolution will be probably known much better in the foreseeable future. In contrast, it is not clear whether we will ever understand the driving forces behind human evolution, in particular, behind the origin of our amazing cognitive abilities.