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Fundamentals

(Universal Phylogenetic Tree)

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Taxonomy of Living Organisms: The Tree of Life

In his *Origin of Species*, Charles Darwin wrote (1859): "Probably all of organic beings which have ever lived on this Earth have descended from some primordial form." Thus, if all living organisms are derived from a common ancestor, in theory it should be possible to establish their relationship (taxonomy) based on the type and number of characteristics they share. This poses enormous difficulties, because data about previously living organisms are restricted to scanty records. But phylogenetic relationships can be based on anatomical features, proteins, DNA, or other molecules (phylogenomics, Delsuc et al., 2005). There is overall agreement that the earth is a little more than 4.5 billion years old and that early forms of life date back about 3.5 billion years.

A. The three domains of living organisms

The formal evolutionary hierarchy of groups of organisms proceeds from the largest to the smallest groups: domain – kingdom – phylum – order – class – family – genus – species. Living organisms are grouped according to the type of cells they consist of, either *prokaryotic* cells or *eukaryotic* cells. Prokaryotes have a simple internal architecture without a nucleus. Eukaryotes have a distinct internal structure with a nucleus containing the genetic material. A third group of living organisms was recognized in the late 1960s, the *Archaea* (also called archaebacteria). They differ from ordinary bacteria by their plasma membrane (isoprene ether lipids rather than fatty acid ester lipids) and lifestyle. They are assigned to two classes, *Crenarchaeota* and *Euryarcheota*.

Archaea can live without molecular oxygen at high temperatures (70°C–110°C, thermophiles) or at low temperatures (psychrophiles), in water with high concentrations of sodium chloride (halophiles) or sulfur (sulfothermophiles), in a highly alkaline environment (pH as high as 11.5, alkaliphiles) or in acid conditions with pH near zero (acidophiles) or a combination of such adverse conditions that would boil or dissolve ordinary bacteria. It is assumed that prokaryotes predate eukaryotes, and that two preexisting prokaryotes contributed their genomes to the first eukaryotic genome. Eukaryotes consist of several kingdoms, including animals, fungi, plants, algae, protozoa, and others. The three domains have a presumed common progenitor, called the last universal common ancestor.

B. Phylogeny of metazoa (animals)

The phylogeny of metazoa differs, depending on whether it is based on the traditional interpretation or on molecular evidence as revealed mainly by rRNA sequence comparisons. Here a simplified version of the molecule-based interpretation is shown.

C. Mammalian phylogeny

Mammals arose about 100 million years ago in the late Mesozoic period of the Earth. The time scale is only approximate. Of the 4629 known mammalian species, 4356 are placentals, which fall into 12 orders. The first five placental orders according to their number of species are rodents (2015), followed by bats (925), insectivores (385), carnivores (271), and primates (233). (Figures modified from Klein & Takahata, 2001.)

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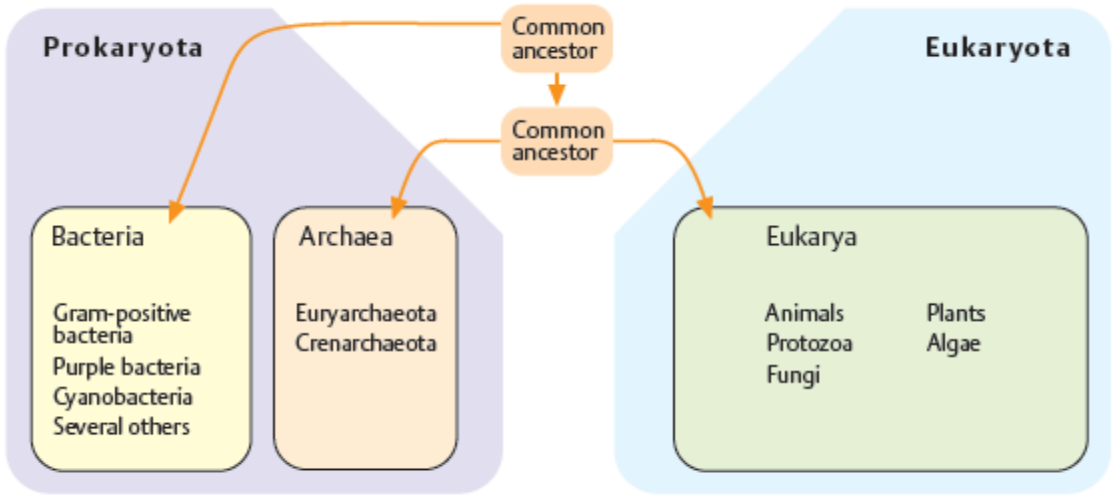
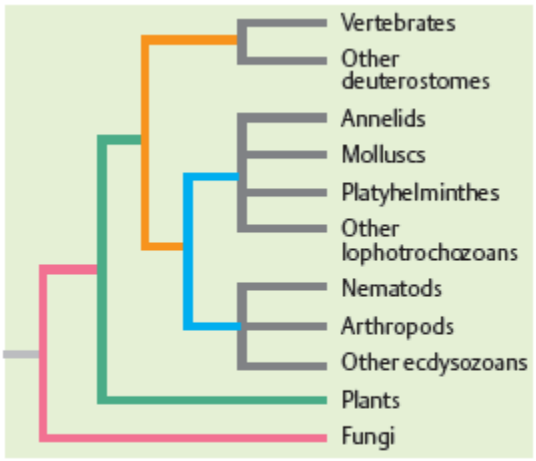
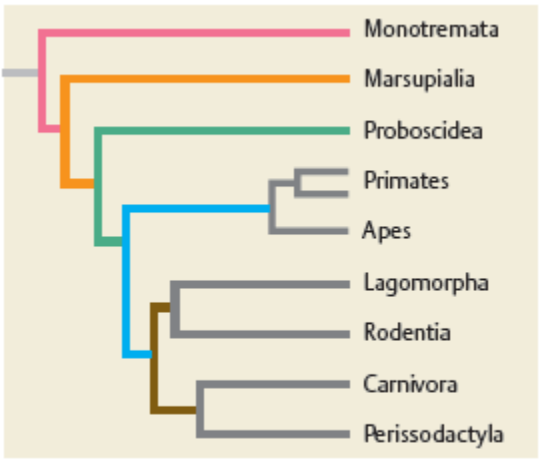


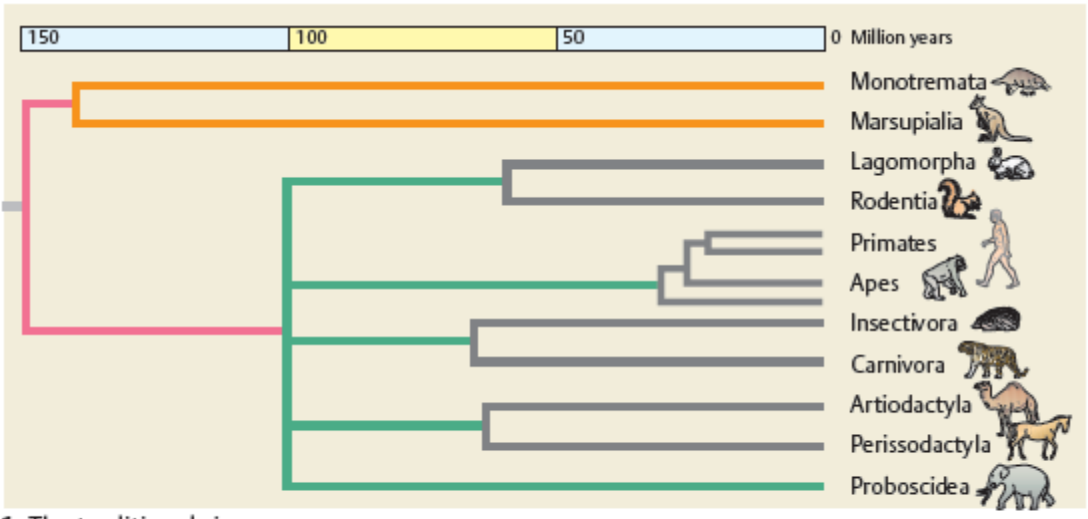
A. Three domains of living organisms (simplified version)



B. Phylogeny of metazoa, simplified

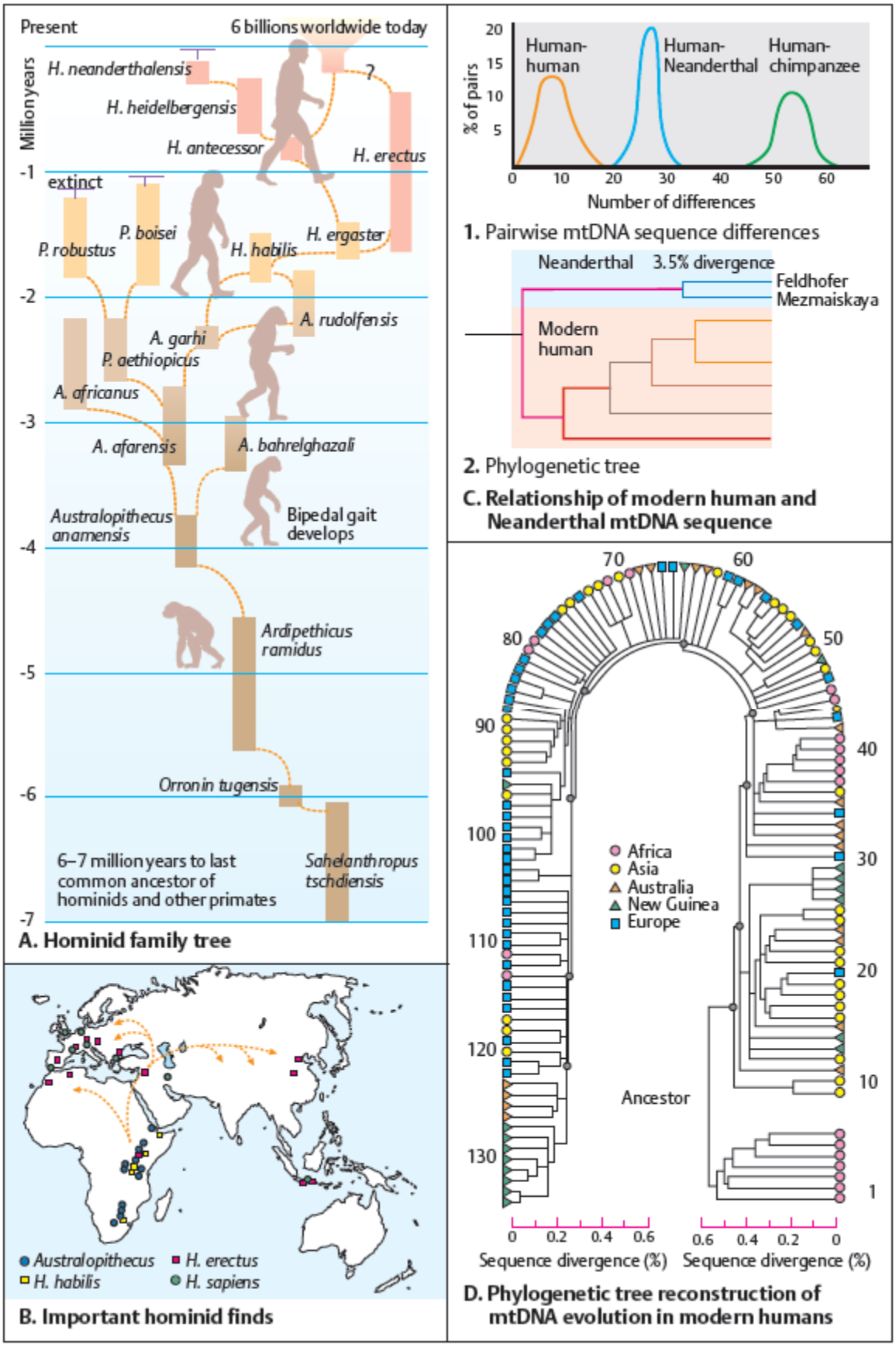


2. The molecular interpretation



1. The traditional view

C. Mammalian phylogeny (simplified)


Present
6 billions worldwide today
Million years
H. neanderthalensis
H. heidelbergensis
H. antecessor
?
H. erectus
-1
extinct
P. robustus
P. boisei
H. habilis
H. ergaster
-2
A. rudolfensis
A. garhi
P. aethiopicus
A. africanus
-3
A. afarensis
A. bahrelghazali
Australopithecus anamensis
Bipedal gait develops
-4
Ardipethicus ramidus
-5
Orronin tugensis
-6
6–7 million years to last common ancestor of hominids and other primates
Sahelanthropus tschdiensis
-7
A. Hominid family tree
Australopithecus
H. erectus
H. habilis
H. sapiens
B. Important hominid finds
% of pairs
Human-human
Human-Neanderthal
Human-chimpanzee
Number of differences
1. Pairwise mtDNA sequence differences
Neanderthal
3.5% divergence
Feldhofer
Mezmaiskaya
Modern human
2. Phylogenetic tree
C. Relationship of modern human and Neanderthal mtDNA sequence
Africa
Asia
Australia
New Guinea
Europe
Ancestor
Sequence divergence (%)
Sequence divergence (%)
D. Phylogenetic tree reconstruction of mtDNA evolution in modern humans

Human Evolution

Humans are the only living species, *Homo sapiens*, within the family of *Hominidae*. All available data are consistent with the assumption that today's humans originated in Africa about 100000–300000 years ago, spread out over the earth, and populated all continents.

A. Hominid family tree

The last common ancestor of man and the chimpanzee lived about 6–7 million years ago (mya). The oldest identified hominid skeletal remains were found in Eastern Africa, in Chad (*Sahelanthropus tchadensis*) in 2002 (ca. 6–7 mya) and Kenyia (*Orronin tugensis*, ca. 5.8–6.1 mya). Fossils from 5 and 4 mya belong to the genus *Australopithecus*. A member of this group is *Ardipethicus ramidus* (ca. 4.5 mya). Bipedal gait developed early, about 4.5 to 4 mya. Several different species originated about 4.5 to 2 mya. The best known is *A. afarensis*, represented by the famous partial skeleton "Lucy" (3.2 mya), with signs of bipedalism. During the Pliocene epoch (5.3 to 1.6 mya) fundamental changes in morphology and behavior occurred, presumably to adapt to a change in habitat, from the forest to the plains: after early bipedalism, brain volume increased dramatically, accompanied by tool making and other complex behavior. Modern humans as they exist today date back about 30000–40000 years. They arrived on the five continents at different times.

B. Important hominid finds

The transition from *Homo erectus* to *Homo sapiens*, i.e., the origin of modern humans, likely occurred according to one of two models: (i) a multiregional model, assuming several transitions, at different times and locations, or (ii) an "out-of-Africa" model, proposing that the transition occurred recently (< 200000 years ago), only once, in Africa. Genetic data favor the out-of-Africa model. (Figure adapted from Wehner & Gehring, 1995)

C. Neanderthals

Modern humans and Neanderthals coexisted about 30000–40000 years ago, but according to genetic data did not interbreed. Pairwise comparison of mitochondrial DNA (mtDNA, see p. 130) of humans, Neanderthals (DNA extracted from fossils), and chimpanzees indicates that Neanderthals did not contribute mitochondrial DNA to modern humans (**1**). At three locations about 2000 km apart (Feldhofer Cave, Neandertal; Mezmaiskaya Cave, northern Caucasus; Vindija, southern Balkans), mtDNA from Neanderthal specimens shows little diversity (3.5%) compared with that of modern humans (**2**). Preliminary data from Y-chromosomal sequences confirm the differences between Neanderthal and human DNA also in the Y chromosome (Dalton, 2006). (Figures adapted from Krings et al., 1997.)

D. A phylogenetic tree

Studies of the Y chromosome (inherited through fathers only) and mitochondrial DNA (inherited through mothers only) are consistent with the out-of-Africa hypothesis. Construction of a phylogenetic tree from the mtDNA of 147 modern humans of African, Asian, Australian, New Guinean, and European origin could be traced to an ancestral haplotype dating back about 200000 years (Cann et al., 1987). Although this result (dubbed "mitochondrial Eve") remains controversial, the major conclusion that there is a recent African origin has been supported. (Figure adapted from Cann et al., 1987).

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