
Contents

1	Evolution, genetics, and systematics	1
1.1	The theory of evolution	1
1.2	Population and evolutionary genetics	6
1.3	Taxonomy	29
1.4	The study of the fossil record	40
2	Taxonomy	45
2.1	Taxonomic considerations of the tribe Hominini	45
2.2	Traits of the human lineage	54
2.3	Beyond morphology: fossil footprints	65
2.4	Bipedalism and adaptation	71
3	The hominin lineage	78
3.1	The origin of hominins	78
3.2	A scenario for the human evolution	83
3.3	The Rift Valley site	91
3.4	South Africa sites	107
3.5	Sites to the north of the Rift Valley	120
4	Miocene and Lower Pliocene hominins	124
4.1	Miocene hominins	124
4.2	The role of locomotion in the divergence of hominoid lineages	134
4.3	Change in the Lower Pliocene: genus <i>Australopithecus</i>	140
4.4	<i>Australopithecus afarensis</i>	142
4.5	<i>Australopithecus anamensis</i>	150
4.6	Miocene human genera	153
4.7	First phylogenetic changes in the tribe Hominini	154
4.8	Phylogenetic relationships of the Miocene and Lower Pliocene hominins	157
5	Middle and Upper Pliocene hominins	160
5.1	What can be included in <i>Australopithecus</i> ?	160
5.2	<i>Australopithecines</i> found outside the Rift: South Africa	161
5.3	<i>Australopithecines</i> found outside the Rift: Chad	166
5.4	The diversification of <i>Australopithecus</i> in the Rift Valley during Middle and Upper Pleistocene	167

5.5	Adaptation; an Upper Pliocene difference	169
5.6	Dental enamel and diet	169
5.7	The genus <i>Paranthropus</i>	172
5.8	Consistency of the evolutionary scheme for the “gracile” and “robust” australopithecines in the Middle and Upper Pliocene	182
6	The emergence of the genus <i>Homo</i>	192
6.1	<i>Homo habilis</i>	192
6.2	The taxon <i>Homo rudolfensis</i>	203
6.3	<i>Homo gautengensis</i>	210
6.4	<i>Homo naledi</i>	211
6.5	<i>Homo georgicus</i>	215
6.6	The transition to <i>Homo</i>	220
6.7	Monophyly of the first <i>Homo</i>	222
6.8	The geographical issue—dispersal of ancient hominins in Africa	225
7	Lithic traditions: tool-making	229
7.1	Pre-cultural uses of tools	230
7.2	Taphonomic indications of culture	233
7.3	Mode 1: Oldowan culture	234
7.4	The transition Mode 1 (Oldowan) to Mode 2 (Acheulean)	239
7.5	Beyond tools: the use of fire	250
7.6	The transition Mode 2 (Acheulean) to Mode 3 (Mousterian)	253
7.7	The African Middle Stone Age	261
8	Middle and Lower Pleistocene: the <i>Homo</i> radiation	266
8.1	Is <i>Homo erectus</i> a well-defined species?	266
8.2	The first exit out of Africa	269
8.3	<i>Homo erectus</i> characterization	273
8.4	African specimens (<i>Homo ergaster</i>)	278
8.5	Asian specimens of <i>Homo erectus</i>	282
8.6	The colonization of Europe	304
8.7	An evolutionary model for the hominins of the Lower and Middle Pleistocene	335
9	Hominin transition to Upper Pliocene	345
9.1	European archaic <i>Homo sapiens</i>	346
9.2	African archaic <i>Homo sapiens</i>	357
9.3	African hominins from the Mindel–Riss interglacial period	357
9.4	Asian archaic <i>Homo sapiens</i>	368
9.5	Are the transitional species between <i>Homo ergaster</i> and <i>Homo sapiens</i> necessary?	377
9.6	<i>Homo floresiensis</i>	379

10 Species of the Upper Pleistocene	395
10.1 <i>Homo neanderthalensis</i>	395
10.2 <i>Homo sapiens</i>	415
11 Neanderthals and modern humans: similarities and differences	441
11.1 Genetic distance between <i>Homo neanderthalensis</i> and <i>Homo sapiens</i>	441
11.2 Brain distance between Neanderthals and modern humans	468
11.3 Cognitive distance between Neanderthals and modern humans	474

Glossary

References

Index

495

503

553

1.1 The theory of evolution

All organisms are related by descent from common ancestors. Humans and other mammals descended from shrew-like creatures that lived more than 150 million years ago; mammals, birds, reptiles, amphibians, and fishes share as ancestors aquatic worms that lived 600 million years ago; and all plants and animals derive from bacteria-like microorganisms that originated more than 3 billion years ago. Biological evolution is a process of descent with modification. The process consists of two components: lineages of organisms change through the generations (anagenesis or phyletic evolution); diversity arises because the lineages that descend from common ancestors diverge through time (cladogenesis or lineage splitting, the process by which new species arise).

1.1.1 Charles Darwin

The founder of the modern theory of evolution was Charles Darwin (1809–82), the son and grandson of physicians. He studied as a medical student at the University of Edinburgh. After two years, however, he left Edinburgh and moved to the University of Cambridge to pursue his studies and prepare to become a clergyman. Darwin was not an exceptional student, but he was deeply interested in natural history. On December 27, 1831, a few years after his graduation from Cambridge, he sailed as a naturalist aboard the HMS *Beagle* on a round-the-world trip that lasted until October 1836. Darwin was often able to disembark for extended trips ashore to collect natural specimens. The discovery of fossil bones from large extinct mammals in Argentina and the observation of numerous species of finches in the Galápagos Islands were among the events credited with stimulating Darwin's interest in how species originate.

The observations he made in the Galápagos Islands may have been the most influential in Darwin's thinking. The islands, in the equatorial Pacific (see map

miles) off the west coast of South America, had been named Galápagos (the Spanish word for tortoise) by the Spanish discoverers because of the abundance of the giant tortoises, different on different islands and different from those known anywhere else in the world. The tortoises sluggishly plodded their way across, feeding on the vegetation and seeking the few pools of fresh water. They would have been vulnerable to predators, but these were conspicuously absent on the islands. In the Galápagos, Darwin found large owls, and mockingbirds, quite different from those found on the South American mainland. Well known is that he found several kinds of finches, varying from island to island in various features, notably their distinctive beaks, adapted to disparate feeding habits: crushing nuts, probing for insects, grasping worms, etc.

In addition to *On the Origin of Species by Means of Natural Selection* (1859), Darwin published many other books, notably *The Descent of Man and Selection in Relation to Sex* (1871), which extends the theory of natural selection to human evolution.

Darwin's theory of natural selection is summarized in *On the Origin of Species* (pp. 80–81) as follows:

Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? If such an occur, we may expect (remembering that more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind. On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection.

The argument consists of three parts: (1) hereditary variations occur, some more favorable than others to the organism; (2) more organisms are produced than can possibly survive and reproduce; (3) organisms