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 *Australopithecus* 140
4.4 Australopithecus afarensis 142
4.5 *Australopithecus anamensis* 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 *Australopithecus*? 160
5.2 Australopithecines found outside the Rift: South Africa 161
5.3 Australopithecines found outside the Rift: Chad 166
5.4 The diversification of *Australopithecus* 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 *Paranthropus* 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 *Homo* **192**

6.1 Homo habilis 192
6.2 The taxon *Homo rudolfensis* 203
6.3 Homo gautengensis 210
6.4 Homo naledi 211
6.5 Homo georgicus 215
6.6 The transition to *Homo* 220
6.7 Monophyly of the first *Homo* 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 *Homo* radiation **266**

8.1 Is *Homo erectus* a well-defined species? 266
8.2 The first exit out of Africa 269
8.3 *Homo erectus* characterization 273
8.4 African specimens (*Homo ergaster*) 278
8.5 Asian specimens of *Homo erectus* 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 *Homo sapiens* 346
9.2 African archaic *Homo sapiens* 357
9.3 African hominins from the Mindel–Riss interglacial period 357
9.4 Asian archaic *Homo sapiens* 368
9.5 Are the transitional species between *Homo ergaster* and *Homo sapiens* necessary? 377
9.6 *Homo floresiensis* 379

10 Species of the Upper Pleistocene 395

10.1 *Homo neanderthalensis* 395
10.2 *Homo sapiens* 415

11 Neanderthals and modern humans: similarities and differences 441

11.1 Genetic distance between *Homo neanderthalensis* and *Homo sapiens* 441
11.2 Brain distance between Neanderthals and modern humans 468
11.3 Cognitive distance between Neanderthals and modern humans 474

Glossary 495
References 503
Index 553