II.18

Human Evolution
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Living humans are the sole living representatives of a lineage, the hominins, which diverged from other living apes 5 to 7 million years ago. Hominins remained limited to Africa for two-thirds of their history. With chimpanzee-sized bodies and brains, early hominins diversified into several lineages with different dietary strategies. One of these found a path toward technology, food sharing, and hunting and gathering, giving rise to our genus, *Homo*, approximately 2 million years ago. As populations of *Homo* spread throughout the world, they gave rise to regional populations with their own anatomical and genetic distinctiveness. Within the last 100,000 years, a massive dispersal of humans from Africa absorbed and replaced these preexisting populations. In the time since this latest emergence from Africa, humans have continued to disperse, interact, and evolve. The rise of agricultural subsistence shifted human ecology, fueling evolution.

GLOSSARY

Acheulean. A style of stone tool manufacture associated with early humans (*Homo erectus*) during the Lower Stone Age era across Africa and Eurasia. Acheulean technology is derived from the older, Oldowan technology and is a progenitor of the more complex stone tools that characterize the Middle Stone Age.

Australopithecines. Members of the hominin clade with the bipedal gait and dentition of modern humans, but lacking the enlarged brains of the genus *Homo*. Australopithecine species have been assigned to a diversity of genera, but most are now included within *Australopithecus*.

Hominins. Modern humans and extinct species more closely related to humans than to chimpanzees or gorillas.

Oldowan. The earliest stone tool industry, which emerged about 2.6 million years ago and persisted until about 1.6 million years ago, when it was replaced by the more sophisticated Acheulean technology.

Orthograde. An upright posture associated with a bipedal gait, such as occurs in modern humans.

Pronograde. The posture of holding the body parallel to the ground, such as is typical of most quadrupedal vertebrates.

While Darwin avoided discussion of the evolution of humans in *On the Origin of Species*, he soon tackled the issue in *The Descent of Man*, which defined the starting point for modern evolutionary anthropology. In the nineteenth and early twentieth centuries, the main theme of anthropology was a perceived lack of fossil progenitors, prompting a much-hyped search for a "missing link." Gradually this concern diminished as paleoanthropologists, especially over the last half century, succeeded in uncovering thousands of fossil specimens, representing diverse human ancestors and collateral relatives. While questions still remain, these fossil data provide a rich history of the origin of many of humanity's distinctive physical traits. Furthermore, archaeological finds have provided information on the behavior of hominins during the last half of human evolution, giving details about diet and social organization. Today, geneticists can add evidence from whole-genome comparisons of living humans, other primates, and some ancient hominins. Through all these lines of evidence a remarkably clear picture of human evolution is now emerging.

We can roughly consider human evolution in three parts. The first, running from 7 million up to around

4 million years ago, saw the origination of the hominin lineage and the initial appearance of our bipedal pattern of locomotion. The second, from 4 million up to around 1.8 million years ago, was the age of the australopithecines. This group of species had a stable set of adaptations in body size and locomotion, while showing substantial dietary and geographic diversity. Our own genus, *Homo*, arose about 1.8 million years ago from the australopithecines. The spread of *Homo* throughout the world, along with many later dispersals and population expansions, laid the foundation for today's human populations.

1. ORIGIN OF THE HOMININS

Chimpanzees and bonobos are our closest relatives among living primates. Whole genome comparisons suggest that our common ancestors with these apes lived between 4 million and 7 million years ago. Our common ancestors with gorillas lived a bit earlier, within the last 10 million years, and with orangutans even earlier, before 12 million years ago. Hence it is during the period between 10 million and 4 million years ago that paleontologists look for the immediate precursors of the hominin lineage.

A rich record of fossil apes has been recovered from the Miocene geological epoch, which lasted from 23 million to 5.2 million years ago. Before 15 million years ago, all known apes lived in Afro-Arabia. Early in the Middle Miocene, some apes dispersed into Asia and Europe, including the Asian ancestors of orangutans. Miocene apes ranged extensively in body size and adaptive niche, and evolved a diversity of locomotor strategies. Many were pronograde quadrupeds, essentially like living Old World monkeys such as macaques and baboons. A few had shoulders and vertebral columns, indicating an orthograde posture or climbing, but no early apes are known to have had the long arms and below-branch suspensory capability of today's great apes. Vertical, orthograde posture was once thought to be an ancestral feature of all apes (including humans); however, some anthropologists now believe that this suspensory body plan evolved convergently in the African and Asian apes.

Living humans are obligate bipeds, with pelvis, foot, and vertebral adaptations that impede effective quadrupedal gait and climbing. The origin of hominins is entangled with this unique adaptation, but the earliest members of our lineage surely did not have the full package of bipedal adaptations found in later hominins. All living apes can move bipedally, and some Miocene apes such as *Oreopithecus* may have specialized in terrestrial bipedality. Recognizing the beginnings of the hominin adaptation to bipedality has been central to identifying early hominins, whose identity remains subject to debate.

The earliest candidate fossils for being hominins share a suite of dental resemblances with later members of our lineage, including small canine teeth, low-crowned molar teeth, and thick molar enamel. Some paleoanthropologists suggest that such dental traits are shared much more broadly with other Miocene lineages, and may not indicate hominin affinities. Skeletal adaptations to upright posture and bipedal stance provide strong evidence that later fossils, after 4.2 million years ago, are human relatives. For earlier fossils, evidence of posture and stance is more equivocal. *Sahelanthropus tchadensis* from north central Africa is the earliest known, at around 7 million years ago. Represented by a nearly complete skull and jaw, it shows an orthograde placement of the skull atop the spinal column. *Orrorin tugenensis*, from western Kenya dating to 6 million years ago, also has a femur consistent with bipedal weight bearing. *Ardipithecus kadabba*, 5.5 million years old from Ethiopia, combines the aforementioned hominin dental features with a toe bone, suggesting that the toe generated force during bipedal walking, as occurs in modern humans. It remains unclear whether these fossil taxa lived before or after the divergence of the human and chimpanzee lineages, and if after, whether they are on the human or chimpanzee side of this evolutionary split.

Ardipithecus ramidus, dating to 4.4 million years ago from Ethiopia, comprises a large fossil sample including one nearly complete skeleton. From its limb proportions, grasping feet, and apelike hands, *Ardipithecus* was a habitual quadruped that also had good climbing abilities. But several of its features are similar to those of hominins, including a shortened pelvis and an upright posture. The teeth and jaws of *A. ramidus*, like those of earlier *A. kadabba*, are among its most hominin-like features. It is often interpreted as the earliest well-documented member of our lineage. However, the data do not rule out the possibility that it is an early member of the chimpanzee or gorilla lineages.

Australopithecines

The first fossils to show clear evidence of a commitment to terrestrial bipedal locomotion are assigned to *Australopithecus anamensis*. Between 4.2 and 3.9 million years ago, this species existed in East Africa. After this time, the same region was inhabited by *Australopithecus afarensis*, which is present in more than a dozen fossil-bearing localities representing hundreds of known specimens, all dated between 3.9 and 2.9 million years ago. The teeth of these two closely similar species show several temporal trends, toward larger postcanine teeth and

functional changes in the canine-premolar cutting anatomy. Because of these trends, most paleoanthropologists regard *A. anamensis* and *A. afarensis* as successive members of a single evolving lineage.

Other lineages of hominins may have been present at the same time, including *Kenyanthropus platyops* from Kenya and *Australopithecus bahrelghazali* from Chad, both between 3.5 and 3.3 million years ago. These are possibly distinct from *A. afarensis* because of cranial and dental peculiarities, but in each case the single specimen is fragmentary. Likewise, a partial foot skeleton from Woranso-Mille, Ethiopia, may represent yet another lineage with a distinct locomotor strategy, possibly a direct descendant of earlier *Ardipithecus*.

A diversity of contemporaneous forms is much clearer among the hominins near the Plio-Pleistocene boundary. From approximately 2.8 to 2.3 million years ago, South Africa was the home of *Australopithecus africanus*, also represented by large fossil samples and in most respects similar in cranial anatomy and teeth to *A. afarensis*. Additionally, by 2.5 million years ago, the robust australopithecines appeared in East and later in South Africa. *Robust* refers to the chewing mechanics of these hominins, which combined powerful jaw muscles with extraordinarily large molar and premolar teeth. The robust australopithecines had approximately the same body size as other australopithecines but clearly had a different diet, featuring many more leaves and hard seeds. *Australopithecus robustus* was a South African form, apparently descended from *A. africanus*. *Australopithecus boisei* was the apex of this trend toward plant dietary specialization, and constitutes the majority of hominin fossils from East Africa between 2.5 and 1.5 million years ago.

The australopithecines were obligate bipeds, meaning their skeletal adaptations to bipedality precluded effective quadrupedal movement. Their feet had a first toe aligned with the other toes, minimal opposability or grasping ability, and arches similar to the feet of living people. Their knees were angled to promote effective weight support in a bipedal stance, and did not rotate to facilitate grasping with the feet. In contrast to nonhuman apes, humans and australopithecines have short hipbones that make a broad, bowl-shaped structure to support the viscera when upright. In addition, the broader hip and shorter ischium enabled effective muscle control of the lower limbs during bipedal walking and running. Our bipedal form of locomotion is not as fast as chimpanzee or gorilla knuckle walking, but it is highly energetically efficient.

However, despite their clear bipedality, australopithecines had relatively long, heavily muscled arms, curved toes and finger bones, and a long clavicle and apelike shoulder blade, all suggesting that climbing remained important to *A. afarensis* and *A. africanus*, even as these hominins moved into more open grassland settings. Still, with hands and legs ill suited for suspension or above-branch quadrupedal walking, early hominins must have climbed in a manner analogous to recent humans. With female masses around 35 kg and males up to 50 kg, they approximated living chimpanzees in body size. The most complete skeletal individuals, such as the "Lucy" skeleton of *A. afarensis*, had statures of 100 to 140 cm, much shorter than the average of any recent human population. Australopithecines had small brains, approximately 450 ml on average, which contrasts with the 1350 ml brains of living humans.

2. EARLY *HOMO*

By 1.8 million years ago, a very different kind of hominin had emerged and spread into Eurasia. *Homo erectus* was the size and stature of recent human hunter-gatherer populations, bigger than any known australopithecine. The skulls of *H. erectus* also contained disproportionately larger brains than australopithecines, initially between 600 and 900 ml, and relatively small teeth. The earliest clear fossil evidence of *H. erectus* occurs at Dmanisi in the Republic of Georgia and Modjokerto, Java, with additional fossil discoveries in East and South Africa. In each of these areas, remains of *H. erectus* existed along with evidence of stone tool manufacture and transport of stone. The evidence indicates that *H. erectus* relied on a higher-quality diet including meat, which imposed greater demands on technical abilities and social organization, but created opportunities for dispersal and range expansion, explaining the species' extra-African distribution.

At present, identifying the population that gave rise to *H. erectus* is one of the most engaging problems in the study of human evolution. Stone tools are known from several sites in Ethiopia and Kenya before 2.5 million years ago, and cut marks on animal bone indicate that these tools were often used for butchering animals. Between these earliest stone tools and the appearance of clear examples of *Homo* fossils lie nearly 700,000 years of time, during which the distinctive features of *H. erectus* must have been evolving, but the identity of the organisms themselves remains mysterious. Between 1.9 and 1.5 million years ago, a number of fossil crania and a handful of partial skeletons may represent a species known as *Homo habilis*. The crania have larger brains than typical for australopithecines, ranging from 500 to 750 ml, and their teeth and jaws are smaller than earlier australopithecines. Still, it remains unclear whether *H. habilis* was ancestral to *H. habilis*, and scholars disagree about how many species these early specimens represent.

Australopithecus sediba is an exceptionally interesting sample, dating to 2 million years ago from Malapa, South Africa. Two very complete skeletons of this species combine *Homo*-like teeth and hands with the body proportions, brain size, and possible arboreal adaptations of earlier hominins. Whether this species could be ancestral to *H. erectus* or *H. habilis* or both could be influenced by analysis of a handful of fossil fragments from East Africa. These have, in the past, been assigned to *Homo*, but until more is known about their anatomy, it will be difficult to test hypotheses about their relationships.

The expansion of brain size from *Australopithecus* to *Homo* is correlated with many aspects of life history and behavior. Neural tissue imposes a high metabolic cost, which humans met by adopting dietary and behavioral strategies that provide high caloric returns. The first postnatal year of human brain development includes a rapid expansion of brain size and concomitant shape changes, in contrast to developmental trajectories of other primates. Neural development in humans extends across a long childhood, with late sexual maturation and an adolescent growth spurt. These ontogenetic patterns appeared in concert with increasing brain size in Pleistocene humans. An increased dependence in hunting and meat scavenging compared to other primates yielded a net increase in diet quality, but imposed several risks, such as competition with large carnivores, unreliability of game, and long training necessary for skill development. Modern humans mitigate these risks by food sharing, sexual division of labor, and gathering of plant foods and animal resources including honey. Hunter-gatherer social groups are relatively egalitarian, with decision making regulated by a coalition of many group members. In this setting, learning of social rules and communication about social norms are fundamental determinants of survival and reproduction. This social environment is thought to be a major selective driver of larger brains that allowed for more sophisticated communication and inferences about the intentions of other social actors. Whereas australopithecines had vocal tracts similar in form to those of chimpanzees and gorillas, early *Homo* had both vocal and auditory traits that could have supported humanlike sound production and reception.

After its origin, *Homo* diversified into regional populations with some morphological differences. In East Asia, *Homo erectus* occupied a range from north China to Java, which was connected to the Asian mainland during periods of low sea level. Across this range, populations developed regional variation in the shape of the browridge and forehead, extent of muscle development of the jaw and neck, and shape of the teeth. Some of these people made a deepwater crossing to the island of Flores by 1 million years ago, where later they may have evolved into a late-surviving isolated dwarf population called *Homo floresiensis*.

In Africa, the fossil record is sparser but supports the idea that *Homo* increased in variability in the period after 1.2 million years ago. The West and South Asian archaeological records show that these regions were also occupied by early human populations, but scant fossils remain. Europe was inhabited by 1.2 million years ago, but the skeletal record represents chiefly the last 800,000 years.

Everywhere they lived, humans used stone tools. The basics of production involved the procurement of stone raw material either from rocky outcrops or from rounded cobbles in streambeds. People were selective about material, choosing fine-grained stone with predictable fracture dynamics, which they sought and transported over kilometers. Removing a sharp flake by itself yields a reliable cutting edge; removing several flakes from a rock, or "core," can shape an edge suitable for chopping or piercing bone. This basic technological pattern is called Oldowan. After 1.6 million years ago, however, mainly in Africa and later in Europe and West Asia, people shaped core tools into symmetrical tools with long edges, called hand axes. The resulting Acheulean stone industry persisted for some 1.3 million years. Along with stone, archaeologists know that Pleistocene humans often used fire, wooden spears and other implements, and sometimes tools made of bone.

By 300,000 years ago, brain size had increased the range of *Homo* to between 800 and 1300 ml. Most paleoanthropologists refer these later remains to species other than *H. erectus*. In Africa and Europe, they are often called *Homo heidelbergensis*, while many scientists call them "archaic *Homo sapiens*." Whatever they are called, these people began to experiment with different technical forms, including a process of stone tool manufacture known as a *prepared core* technique. The result was a greater control over the shape of end products, sometimes yielding blades and points that were attached (hafted) onto spears as compound tools. These stone industries are called Middle Stone Age (MSA).

3. NEANDERTHALS AND THE ORIGIN OF MODERN HUMANS

Genetic evidence has greatly clarified our understanding of the human populations of the last 250,000 years. Archaeology and skeletal remains help to complete the story, adding perspective on the causes and timing of the key events. This was a time of vast migrations and mixture of distant populations with each other.

By 250,000 years ago, MSA people had developed regional tool industries with little evidence of interregional

movement or exchange. A small skeletal sample represents these MSA populations from across Africa. These represent the earliest humans with modern anatomical characteristics, including a high forehead, face tucked beneath the front of the braincase, and a rounded cranial vault. The functional import of these changes is not yet understood, but they seem to reflect a basic shift in developmental patterning.

The later MSA peoples, after 120,000 years ago, became regionally differentiated. In both southern Africa and the Maghreb, people collected shells and marked objects, for example, with natural pigments and ostrich eggshells. In Mozambique, people gathered large stores of wild grains; in Ethiopia, they transported obsidian over hundreds of kilometers.

Some African population dispersed into West Asia by 105,000 years ago, taking with it a subset of the genetic variation present in Africa. In western Asia and Europe they encountered the Neanderthals, whose remains are dated between 200,000 and 300,000 years ago. Beginning from a common anatomical background with modern humans, Neanderthals evolved a number of traits that appeared nowhere else: long, barrel-shaped skulls with a rearward projection called an "occipital bun," thick curving long bones with large joints, and at least in the European part of their range, body proportions now associated with inhabitants of very cold environments. Neanderthals were a small population dispersed over a large space, and even more than their contemporaries in Africa, depended heavily on meat from large prey animals. The Neanderthals were probably a minor component of the overall Pleistocene human population, but their skeletal and archaeological remains are numerous, so we understand their lifeways better than other populations. Additionally, it has proved possible to obtain a partial genome sequence from Neanderthals, which has shed great light on the genetic ancestry of modern humans outside of Africa.

A sign of the weaknesses of the skeletal record is the Denisova genome, from the Altai Mountains of southern Siberia. This genome represents a population living at the same time, but to the east of the Neanderthals, but substantially distinct from the known Neanderthals genetic sample. Living people in Australia and New Guinea derive around 5 percent of their ancestry from a population similar to the Denisova individual. Neanderthals themselves contributed between 2 and 4 percent of the ancestry of present populations throughout the world (including Australasia), except within Africa itself. These genetic results may help to explain morphological features that imply some degree of regional continuity of human populations in Europe, East Asia, and Australasia; however, the spread of Africans within the last 100,000 years accounts for more than 90 percent

of the ancestry of living people, but a small multiregional component of ancestry has remained in the face of this and subsequent migrations.

4. RECENT HUMAN EVOLUTION

After modern human populations became established throughout the world, evolution continued to shape our biology. Early human populations in Europe and northeast Asia likely found themselves poorly suited for the low temperature and insolation of these regions. The tropical regions of Asia had a similar physical geography but very different floral and faunal communities than Africa. Watercraft allowed people to colonize Australia, Melanesia, and other island regions, and facilitated the migration of people from the Bering Land Bridge into the southern parts of the Americas before 14,000 years ago. Rapid evolution by natural selection in all these novel environments was inevitable.

As humans dispersed throughout the world, they also increased vastly in numbers. At the end of the last glaciation, people expanded their dietary breadth to a greater number of plant and animal species, a process called the Broad Spectrum Revolution. Some experimented with planting and keeping seed crops; others began managing herd animals more intensively. Over many generations, these processes led to domestication of former wild species, settlement of many human groups into villages and cities, and the rise of political and economic elites. Pastoralists sustained large populations on formerly less hospitable plains and steppes, sometimes migrating over long distances. Civilization was one result of this agricultural revolution; warfare and serfdom were others.

Human skeletal traits (and by inference genes) have changed during the last 20,000 years at a rate unmatched by earlier periods. Humans became more gracile as cranial muscle attachments and structures such as the browridge became lighter. After the introduction of agriculture, smaller teeth and jaws became common, and a higher proportion of individuals failed to develop third molars, or "wisdom teeth," entirely. Along with such evolutionary changes, skeletal samples document the catastrophic health effects resulting from agriculture and village life.

Pathogens have been among the most obvious causes of recent human evolution. For example, more than 20 different alleles that protect to some extent from falciparum malaria are known from different human populations, many of which have arisen within the last few thousand years. Diet is another important cause of recent evolutionary changes, as some human groups have specific genetic adaptations to starchy grains and milk consumption. The physical environment

has exerted its own selection on populations at high altitude, with selection affecting oxygen transport, and at high latitude, with recent strong selection on genes associated with pigmentation.

Industrial populations of the last 200 years have undergone further radical changes in longevity, residence patterns, and family size. Nevertheless, selection and evolution of modern human populations is ongoing, with documented selection on quantitative traits of medical and biometric interest. The future direction of human evolution cannot be predicted from our past history (see chapter VIII.12), but the pace of recent evolution suggests that our species may have many more changes ahead.

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