

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/321392171>

Hominin Evolution

Chapter · January 2017

DOI: 10.1007/978-3-319-16999-6_3416-1

CITATION

1

READS

6,808

2 authors:



[Laura van Holstein](#)

University of Cambridge

12 PUBLICATIONS 176 CITATIONS

[SEE PROFILE](#)



[Robert Foley](#)

University of Cambridge

217 PUBLICATIONS 11,234 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



PhD Thesis [View project](#)



IN-AFRICA Project [View project](#)

Hominin Evolution

Laura van Holstein and Robert A. Foley
Leverhulme Centre for Human Evolutionary
Studies, University of Cambridge, Cambridge,
UK

Synonyms

[Human evolution](#); [Previously hominid evolution](#)

Definition

The evolution of *Homo sapiens*, its ancestors, and closely related species from the last common ancestor with chimpanzees onward (~7 million years ago to present).

Introduction

Early evolutionary biologists answered the question of human origins by searching for the precise location of “man’s place in nature,” in T.H. Huxley’s phrasing, based on comparative anatomy between living species. Research has moved from viewing humanity at the top of the *scala naturae* to seeing it as “just” a big-brained, bipedal primate, and the focus shifted to explaining how we *arrived* at “our” place. The post-nineteenth-century focus has been on

understanding the evolutionary circumstances that produced *Homo sapiens*, based on the idea that human-specific traits are the product of the same evolutionary processes that led to all other species. This effort is notably multidisciplinary: human origins fall within the remit of anthropology, biology, genetics, zoology, primatology, geology, and psychology. The (occasionally contentious) synthesis of work within these fields has produced a coherent, albeit pixelated picture, of which this summary is a sketch. It first reviews hominin evolutionary history chronologically and then explores evolutionary patterns, including the evolution of cognition, in more depth.

Hominin Evolutionary History

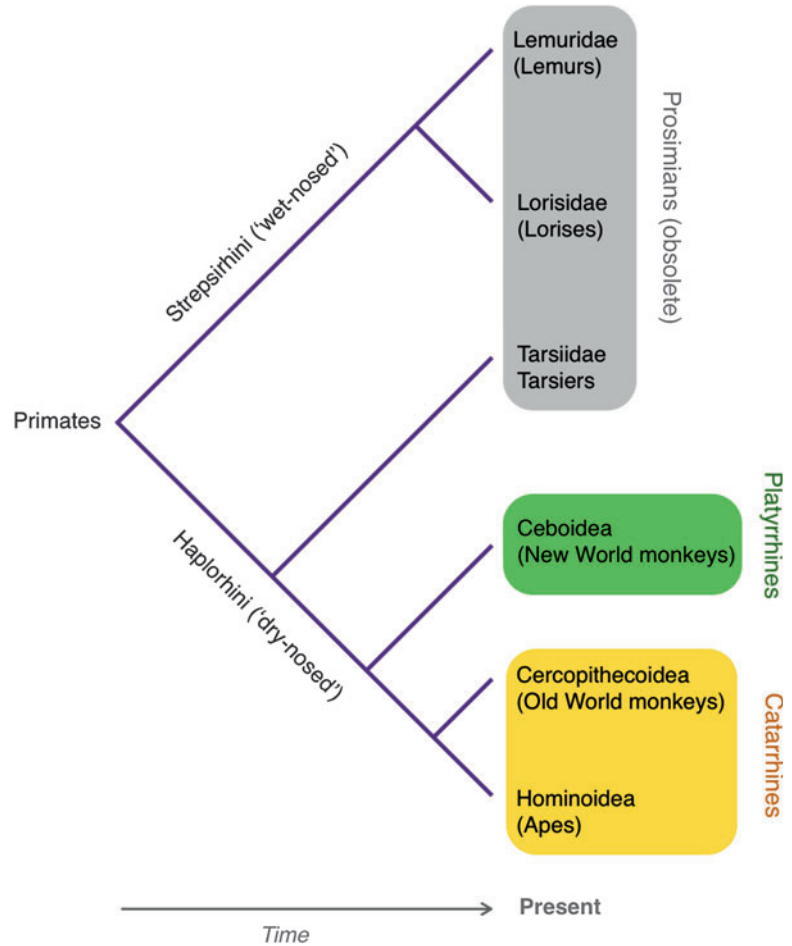
Hominins in Comparative Perspective

Systematics of the Primates

The Order Primates, to which we belong, is characterized by increased body size, dexterous hands, flexible limbs, nails instead of claws, a shortened snout, and associated shift of emphasis from olfactory to visual sensitivity manifested in, for example, stereoscopic vision. Primates are divided into two groups, separated terminologically if rather prosaically by nasal dampness: Strepsirhini (“wet-nosed”) and Haplorhini (“dry-nosed”) (fig. 1). This division was initially based on purely morphological characteristics and was later refined and confirmed using molecular and genetic data. The Strepsirhini, whose

Hominin Evolution,

Fig. 1 Phylogeny of living primates



ranks comprise lemurs and lorises, are characterized mostly by nocturnal adaptations (e.g., eyes with reflective layers to improve night vision), heightened olfactory sensitivity, and comparatively small brains. The Haplorhini are split into three major taxa: tarsiers, platyrrhines, and catarrhines. Current genetic phylogenies place tarsiers within the Haplorhini despite their strepsirhine-like features, but their evolutionary relationship has been debated. The monkey-grade, or simian, primates are again distinguished nasally, but this time by shape: they include platyrrhines (“flat-nosed”) and catarrhines (“down-nosed”). Platyrrhines – of which the only living representatives is the Ceboidea superfamily which includes capuchins, marmosets, and howler monkeys – are restricted to the New World. They are mostly arboreal and are the only group to include monkeys with prehensile tails. Catarrhines, by

contrast, are found in Africa and Asia: these are the Old World monkeys (Cercopithecoidea) and apes (Hominoidea). The Old World monkeys are unlike the apes in that they have tails, and include baboons, mandrills, and macaques. The Hominoidea comprises the arboreally specialized lesser apes (gibbons, or Hylobatidae) and great apes (Hominidae). Humans are therefore catarrhines, hominoids, and hominids.

Outline of Primate Evolution

There is an element of arbitrariness inherent in the idea of a “beginning” of the evolution of a lineage: after all, evolution is a continuous process, and consequently there are no real starting points within it. For this reason, the evolutionary events (like the splitting of lineages) requiring

chronological estimates are based on *taxonomic* frameworks.

The current chronological outline of primate evolution is based on convergences between anatomical, fossil, and molecular approaches, of which the “molecular clock” gives the most frequently used dates. By assuming a constant rate of mutation during evolution, the molecular clock uses similarities and differences between biomolecules to estimate lineage-split times. The divergence between primates and closely related lineages is estimated somewhere between 70 and 80 Ma, in the Cretaceous epoch. The Strepsirhini and Haplorhini diverged from each other around 55–90 Ma, and recent genetic estimates suggest they last shared a common ancestor ~87 Ma, at the very beginning of the primate radiation. Debate continues about the most likely location of their common ancestor – but Asia is a strong contender, because the basal clades of both lineages (the haplorhine tarsiers and strepsirrhine lorises), as well as the closest relatives of primates, Dermoptera and Scandentia, are exclusive to Asia. Fossil evidence of this common ancestor remains elusive. Tarsiers diverged from the rest of the Haplorhini early, around ~81 Ma. Platyrrhines last shared a common ancestor with catarrhines ~43 Ma, but the fossil record is equivocal about where this last common ancestor lived and the platyrrhine route of dispersal to the Americas is therefore also unclear. Platyrrhines remained entirely arboreal, whereas some catarrhines (including humans) adapted to a terrestrial life. The Catarrhini further subdivided into Cercopithecoidea and Hominoidea ~25 Ma. Within the Hominoidea, the consensus order of divergence is an early Hylobatidae (gibbon) split with the rest of the clade at ~21 Ma, followed by *Pongo* (orangutan) at ~15 Ma and *Gorilla* at 8–9 Ma, and a final split between the *Pan* (chimpanzee and bonobo) and *Homo* lineages between 6 and 7 Ma.

Hominin Relationships to African Apes

Collectively, all modern and extinct great apes, including humans, are currently referred to as *hominids*. The African contingent of the family Hominidae (comprising *Homo*, *Pan*, and *Gorilla*)

is known as the subfamily Homininae. Within the Homininae there are three tribes: Gorillini, Panini, and Hominini. Humans are therefore most closely related to the two *Pan* species, chimpanzees and bonobos

Previously, “hominid” was also used to refer to the human lineage, including our ancestors and related species, after the split from *Pan*; but nowadays, humans and extinct species more closely related to humans than *Pan* are known as *hominins* (see Fig. 2). In practice, this means that we can start speaking of hominins around 7 million years ago, since molecular dates suggest the Hominini-Panini lineages diverged around this time – although the proposed split times range from 13 to 5 Ma.

Implications for Hominin Origins

In the context of the range of living species, hominins share the closest evolutionary history with the African apes and in particular with chimpanzees and bonobos. This evolutionary proximity implies that features we have in common with all Hominidae genera are the consequence of shared ancestry. The list of shared features, which were presumably present in our common ancestors, has expanded considerably over recent years and now includes behavioral traits, potentially including a capacity for “cultural,” or socially transmitted, behavior (Whiten 2011).

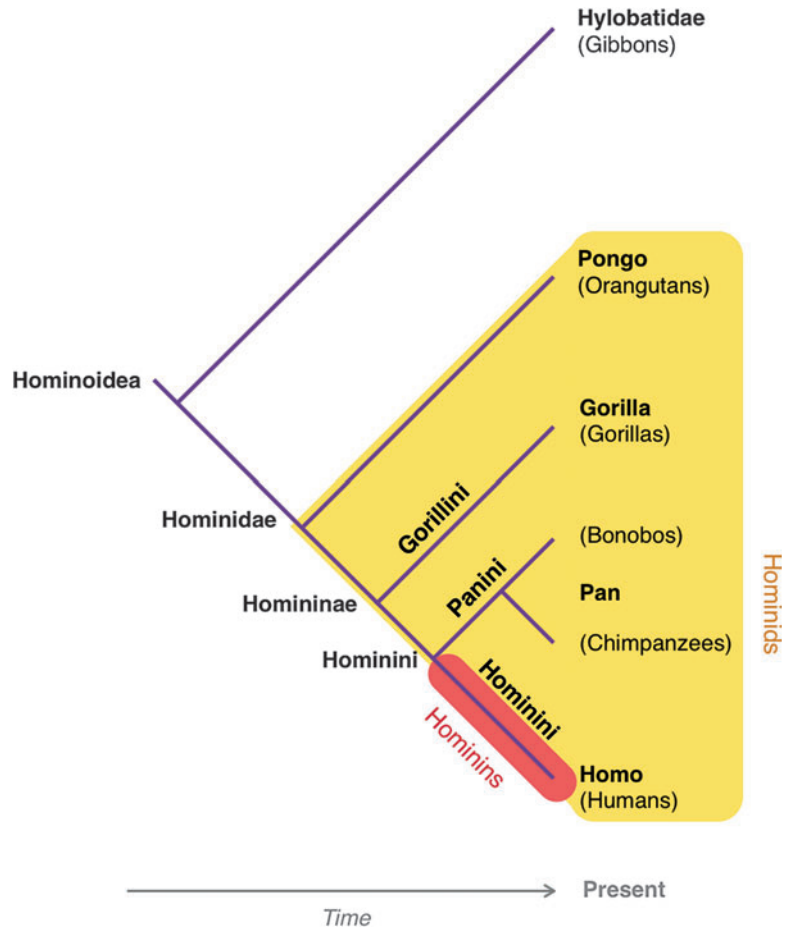
The features *not* shared with African apes are most probably the product of our lineage’s evolution after it diverged from our modern ape cousins’ lineages – in other words, the features that arose specifically during hominin evolution. In this perspective, it is implicit that some features unique to other ape genera are the consequence of their independent evolution, so apes cannot always be used as direct analogues or homologues for human ancestors. This phylogenetic framework is essential in exploring the origins of hominin characteristics, as it is a precursor to discovering *why* and *when* these “human” features appeared and what *consequences* they had.

Environmental Context for Hominin Evolution

The problems to which hominin adaptations provide solutions derive from the physical

Hominin Evolution,

Fig. 2 Hominin relationships to African apes. Within the family Hominidae, the African apes, or Homininae, comprise three tribes: Gorillini, Panini, and Hominini. The term *hominid* is used to refer to all great apes, while *hominin* refers to humans, the direct ancestors of humans, and other closely related species *after* the split from *Pan*



environment: the ecological context in which hominins evolved. Hominins diverged from the Panini clade at the end of the Miocene (23–5.3 Ma), around 7 Ma. Important climatic changes coincide with their emergence: long-term decline in temperatures (culminating in Pleistocene Ice Ages) and associated fragmentation of habitats (involving the breaking up of Miocene tropical forests and expansion of grassland, woodland, and bushland, producing mosaic habitats). These more open environments played significant roles in hominin evolution. Furthermore, the increased fragmentation probably promoted speciation through population isolation and also produced dynamically changing selective pressures associated with changing resource type, distribution, and seasonality.

Hominin Origins

The Hominini-Panini split is poorly documented in the fossil record, reflecting an overall paucity of Miocene fossils. Hominin origins consequently remain an elusive paleoanthropological problem. The problem has two key elements: first, the environmental and evolutionary context in which the split and, second, the lineages involved – the last common ancestor (LCA) of humans and chimpanzees, and its daughter species, the earliest member of the hominin clade.

To date, no potential chimpanzee-human LCA is known from the fossil record. This precludes empirical reconstruction of the context in which the ancestral species split into two independent lineages. Even the geographical context of that group is unclear; although hominins belong to the African ape clade, and this clade might have

a prolonged African ancestry, an alternative scenario is a Eurasian ancestor that migrated back into Africa in the Late Miocene. Two potential Eurasian ancestors have been proposed: *Graecopithecus* and *Ouranopithecus* – but there is insufficient fossil material to conclusively resolve the issue.

There are three African Late Miocene contenders for “early hominin” status: *Sahelanthropus tchadensis* (7.43–6.38 Ma), *Orrorin tugenensis* (6.14–5.52 Ma), and *Ardipithecus* (6.7–4.26 Ma). These three genera are classed as potential basal members of the hominin clade due to probable bipedal adaptations and, where sufficient evidence, dental traits shared with later hominins. Found in Chad, *Sahelanthropus* has an anteriorly positioned foramen magnum (the opening at the base of the cranium through which the spinal cord passes) compared to quadrupedal species, indicating that its head was held on an upright body consistent with some level of bipedal locomotion. However, the incomplete nature of the fossil makes reconstruction of the position of its foramen magnum, along with the behavioral inferences based upon it, contentious. By contrast, East African *Orrorin* is only known from fragmentary postcrania. Its femoral morphology suggests it shared distinctive hip biomechanics with the unequivocally bipedal australopithecines (Richmond and Jungers 2008). Finally, *Ardipithecus*, an Ethiopian genus comprising two species (*ramidus* and *kadabba*), shows a mosaic of terrestrial and arboreal features, indicating it was a facultative biped – in other words, that it moved bipedally on the ground, but quadrupedally in trees. Dentally, *Ardipithecus* showed reduced sexual dimorphism of the upper canine: a hallmark of later hominins, contrasting with marked canine sexual dimorphism in chimpanzees.

Opinions are divided about early hominin taxonomy: the fossils may represent three individual genera, may belong to one basal hominin genus, may not belong to the hominin clade at all, or a combination of these. The real difficulty in assigning Late Miocene apes to a species, genus, or lineage is not just ascertaining the presence or absence of derived traits shared with later

hominins, as their evolution may have been paraphyletic. The divergence of later Miocene African hominids may have involved complex speciation with prolonged gene flow among populations and the evolution of extinct lineages with no direct ancestral relationship to later hominids. Further uncertainties about genetic mutation rates and generation times compound these paleontological considerations, because they influence molecular clock split-time calculations. Slow mutation rates produce dates as early as ~13 mya for the Hominini–Panini split, while fast ones estimate it at ~5 mya.

Early Hominin Evolution

Early hominin evolution (~4.2–2 Ma) is usually taken as synonymous with the emergence, diversification, and partial extinction of the australopithecines, defined broadly (see Table 1). This is correct, in a sense, although there is no clear consensus as to which early hominin species should be included formally in *Australopithecus*. The period might have seen the emergence of at least two other genera: *Paranthropus* (sometimes referred to as the “robust” australopithecines) and *Kenyanthropus*. The exact nature and extent of taxonomic diversity is debated; some researchers advocate a minimal level, but most support at least some degree of diversification. The evolutionary history of the early hominins coincides with the early Pliocene and consequently takes place in the context of increasing habitat fragmentation. In this ecological context, the high degree of species diversity (however it is interpreted taxonomically) during this period is frequently interpreted as an adaptive radiation, although the scale, relative to other primate groups, is relatively small.

As a whole, this diverse group shares bipedal adaptations, reduced canines and canine sexual dimorphism, relatively large postcanine dentition, apelike life histories, body sizes, and cranial capacities. Broadly speaking, the latter three remain relatively constant across early hominin species (see Table 1), while the first two contribute to the fundamental trends underlying australopithecine diversity. These are:

Hominin Evolution, Table 1 Early hominins

Species	Age (Ma)	Mean cranial capacity (cm ³)	Mean body mass (kg)
<i>S. tchadensis</i>	7.43-6.38	365	-
<i>O. tugenensis</i>	6.14-5.52		
<i>Ar. kadabba</i>	6.7-5.11	-	-
<i>Ar. ramidus</i>	4.6-4.26	300-350	32
<i>Au. anamensis</i>	4.37-3.82	-	46
<i>Au. afarensis</i>	3.89-2.9	433	39
<i>Au. africanus</i>	4.02-1.9	454	31
<i>Au. sediba</i>	1.98	420	26
<i>Au. garhi</i>	2.5-2.49	450	-
<i>Au. bahrelghazali</i>	3.85-3.31	-	-
<i>P. aethiopicus</i>	2.73-2.23	443	32
<i>P. boisei</i>	2.5-1.15	493	46
<i>P. robustus</i>	2.27-0.87	536	30
<i>K. platyops</i>	3.54-3.35	Within the range of <i>Australopithecus</i> or <i>Paranthropus</i>	-

Source: Boyle and Wood (2017)

“—” indicates absence of fossil data. Shaded species have been proposed as primitive members of the hominin clade, but their exact phylogenetic affinities are uncertain. Age ranges take into account dating error

1. Varying levels of terrestriality, with morphological adaptations to ground-dwelling. Mosaics of locomotor features are indicative of a spectrum of bipedal adaptation, with species incorporating arboreal climbing in their locomotor repertoire to greater or lesser degrees. *Au. afarensis*, a well-represented species (with around 300 individuals found so far) that lived from 3.89–2.9 Ma, has clear derived bipedal adaptations, like a humanlike pelvis and non-grasping big toe, but also primitive features indicative of arboreality, like long, curved fingers and a strong shoulders. A set of footprints found in Laetoli, Tanzania, dated to ~3.7 Ma and likely made by *Au. afarensis*, are commonly interpreted as the product of a form of bipedalism not unlike that of modern humans (Raichlen et al. 2010). *Au. africanus* (4.02–1.9 Ma) provides evidence of an increased reliance on arboreality than its older relative, with a grasping big toe and longer arm to leg ratio. *Au. sediba* (1.98 Ma) moved with a distinct combination of arboreal and terrestrial features, again implying a unique form of bipedalism (Zipfel et al. 2011). So, while early hominins were clearly united in their increased reliance on bipedal locomotion compared to their Miocene ancestors, accumulating evidence suggests at considerable diversity the *nature* and *degree* of bipedalism each species exhibited.
2. Specialization of subsistence behavior with a trend toward postcanine megadonty. The general “australopithecine” trend toward postcanine megadonty reflects increasing specialization in subsistence behavior over ~2

million years. From an ecological perspective, this makes sense: as new environments (such as those resulting from decreasing temperatures in the Pliocene) become saturated with opportunistic species, the evolutionary advantage shifts to specialized species who extract energy from specific resources more efficiently (Foley 1987). Subsistence specialization is especially pronounced in *Paranthropus* (later “robust” Australopithecines (*aethiopicus*, *boisei*, and *robustus*), ranging from 2.73 to 0.87 Ma), which share adaptations for chewing extremely hard and brittle foods like nuts and seeds. These adaptations include prominent sagittal crests for the attachment of massive chewing muscles, large and robust cheekbones to accommodate these muscles, and thick dental enamel. Some researchers consider their degree of subsistence specialization sufficiently different to that of the “gracile” Australopithecines to suggest they are a separate genus, *Paranthropus*, in accordance with one definition of a genus as a clade sharing a single adaptive zone (Wood and Collard 1999).

The Origins of *Homo*

The exact ancestry of *Homo* is unclear, but the genus tends to be seen as the evolutionary product of the gracile australopithecines. In general, *Homo* differs from *Australopithecus* in its trend toward ecological generalism, reflected in efficient ranging behavior, encephalization, and behavioral flexibility. The candidates at the center of the debate about the origin of our genus, which first appears at the start of the Pleistocene (2.5–0.01 Ma), are *Homo habilis* (2.6–1.65 Ma) and *Homo rudolfensis* (2.09–1.78 Ma). Their status as members of *Homo* is contentious. The problems with assigning fossils from around 2 Ma to either *Homo* or *Australopithecus* are twofold: first, the process of macroevolution and, second, uncertainty regarding the exact defining characteristics of the *Homo* genus.

In a now familiar tune, exact taxonomic affinities between species around this time are hotly debated. This derives, in part, from the debated definition of “genus” in the context of macroevolution, where the central question is *when*

differences between species or groups of species are sufficient to merit their distinction at the generic level and of what *nature* these differences should be. A character-based distinction between *Homo* and *Australopithecus* – where *Homo* is defined on the basis of enlarged absolute brain size ($>600\text{ cm}^3$) and “complex” behavior, including tool use and language – long formed the bedrock of investigation into the origins of *Homo*. This essentially amounts to a “checklist” of features true *Homo* species should exhibit, but its validity has been questioned in recent years.

On the one hand, the apparent simplicity of a trait list for *Homo* membership is deceptive, because inferring the presence or absence of “complex” behavior is difficult. Language leaves no direct trace in the fossil record, and no stone tools have so far been found associated directly with Pliocene hominins. In the context of multiple coexisting hominin species around 2 Ma, this precludes assigning makers to lithic assemblages. The synonymy of technological ability and the *Homo* genus, moreover, is an artifact of the incomplete archaeological record: until 2015 the earliest known stone tool industry was the Oldowan, dated to 2.5 Ma, coincident with the appearance of the first bigger-brained hominin species (*H. habilis*). The beginning of the archaeological record has now been pushed back to 3.3 Ma with the discovery of the Lomekwian industry (Harmand et al. 2015), implying either that *Homo* originated much earlier in hominin evolution or, more parsimoniously, that the evolution of technological behavior preceded the emergence of our genus. Simple stone tool use by chimpanzees and capuchins in order to crack nuts supports the latter.

On the other hand, the usefulness of a trait checklist is undermined because it *oversimplifies* distinctions between genera by assuming a definable moment in time at which these distinctions appeared. This might not have been the case, and it has recently been suggested that the abrupt *Homo-Australopithecus* divide that the checklist approach is based on has been exaggerated and that the emergence of *Homo* from *Australopithecus* is better conceived of as an accumulation of small transitions (Foley 2016).

Hominin Evolution, Table 2 The *Homo* genus

Species	Age	Cranial capacity (cm ³)	Encephalisation quotient	Geography
<i>H. habilis</i>	2.6-1.65	611	~3.6	Africa (Kenya, Ethiopia, Tanzania, South Africa, Malawi)
<i>H. rudolfensis</i>	2.09-1.78	793	~3.8	Kenya
<i>H. erectus</i> *	1.85 Ma - 27 kya	981	~3.6	Asia*
<i>H. ergaster</i> *	2.27 Ma - 870 kya	796	~3.3	Africa*
<i>H. heidelbergensis</i>	700 - 100 kya	1158	~5.3	Eurasia*
<i>H. floresiensis</i>	100 - 60 kya	417	2.5 - 4.6	Flores, Indonesia
<i>H. naledi</i>	~0.3	460 - 610	~2.4	South Africa
<i>H. neanderthalensis</i>	197 kya - 39 kya	1420	~5.5	Europe and Western Asia
Denisovans	50 -28 kya	-	-	Siberia
<i>H. sapiens</i>	200 kya - present	1457	~5.8	Archaic forms evolved in Africa, now worldwide

Sources: Age, Cranial capacity, and Geography from Boyle and Wood (2017); Encephalisation quotients from Schulkin (2011)

* indicates this is debated; see text for discussion. Shaded species have been proposed as the earliest members of *Homo*, but their exact phylogenetic affinities are uncertain

So, theoretical problems abound. What this means in practice for the putative earliest members of *Homo*, *habilis* and *rudolfensis*, is that they likely represent “intermediate” species between *Australopithecus* and *Homo*, with features linking them to both genera. They have larger absolute brain sizes than Australopithecines and likely made and used stone tools, but the *habilis* hand and foot indicate it might have retained some arboreality in its locomotive repertoire. Both species have been suggested to have similar life histories to Australopithecines and certainly have considerably smaller bodies than later *Homo*. A phylogenetic approach to *Homo* by Wood and Collard (1999), where they define a genus as a “monophylum [common ancestor and all descendants] whose members occupy a single adaptive

zone,” suggested *habilis* and *rudolfensis* do not belong in the genus. In summary, the emergence of *Homo* appears to be characterized by greater complexity than previously assumed.

The Evolution of *Homo* in the Pleistocene

After 2 Ma, human evolution is characterized by a general trend toward bigger brains, reduced dentition, increased technological complexity, and the development of a body plan adapted for long-distance ranging (see Table 2 for a list of *Homo* species after 2 Ma). The development of these traits contributed to the first hominin dispersals out of Africa, currently estimated at ~1.8 Ma. Despite these distinct overall patterns, specific evolutionary relationships between hominins in this period are unclear.

While its membership to the *Homo* genus is uncontested (based on its large brain, tool use, and modern body proportions), the precise phylogenetic affinities of *Homo erectus* are not. Its ancestry, descendants, and classification are debated, especially in relation to *Homo ergaster*, which is exclusively found in Africa. Some researchers assign *ergaster* and *erectus* to a single evolving lineage, called *Homo erectus*; others support a variation on this argument, where *ergaster* is the “African variety” of *erectus*. From this perspective, *Homo erectus sensu lato* (s.l.) refers to the lineage as a whole, whereas *Homo erectus sensu stricto* (s.s.) is used to refer to its Asian representatives (Lordkipanidze et al. 2013). Alternatively, *Homo erectus* and *Homo ergaster* can be seen as two distinct species, where *ergaster* is older and African and *H. erectus* younger and Asian (Klein 1999). These contrasting perspectives are based on interpretations of morphological variation between fossil groupings (with the unresolved issue being how much variation can be exhibited within a distinct species unit). An unusually large set of contemporaneous hominins found together in Dmanisi, Georgia, illustrates the complexity. The site was inhabited from 1.8 to 1.7 Ma (making these the earliest hominin fossils outside Africa), and its inhabitants exhibit wide morphological variation with features linking them to *H. habilis*, *H. ergaster*, and *H. erectus* (s.s.). This mosaic suite of features, combined with the range of variation, it has been suggested, shows a single evolving *Homo* lineage with some geographically stratified variation around 1.8 Ma (Lordkipanidze et al. 2013). However, across the range of possible *Homo* paleodemes of the Lower Pleistocene, it is likely that several lineages existed in relative geographical isolation, some becoming established as stable species – for example, *Homo erectus*.

Regardless of systematics, the *Homo* lineage is characterized as a whole by fully modern (i.e., humanlike) bipedalism reflected in a rounded pelvis, long legs relative to arms, and arched feet, as well as reduced postcanine dentition and large brains (~900 cm³). They made simple (Mode 1) stone tools and might have used fire.

Whatever their ultimate phylogenetic status, hominins first dispersed out of Africa in the

Lower Pleistocene. The earliest evidence possible claim for a dispersal are some disputed stone tools from Pakistan (Dennell et al. 1988), at around 2 Ma; a less contested earliest date outside of Africa are from the hominin remains at Dmanisi (1.8 Ma) and lithic assemblages in Israel (1.9–1.7 Ma). There is considerable uncertainty about the timing, route, and direction of early hominin dispersals, but archaeological evidence implies at least three waves of migrations. The first, around 1.8 Ma, involved the makers of Oldowan core-chopper tools; the second, around 1.4 Ma, makers of Acheulean hand axes; and the third, around 0.8 Ma, is represented by Acheulean assemblages with numerous flake cleavers. It is commonly proposed that these dispersals were facilitated by behavioral flexibility (manifested in greater levels of hunting and cooperation and dependence upon technology) resulting from increased intelligence, as well as changes in body plan reflecting adaptations for long-range walking.

The best-known later descendant of these dispersing hominins is the larger-brained *Homo heidelbergensis* (0.7–0.1 Ma). As a whole, this species was larger than preceding hominins, stockily built, and had thick cranial bones and massive brow ridges. Its brain size was almost as large as that of modern humans at around 1200 cm³, although its encephalization quotient (the allometric relationship between the brain and body size) is smaller. Technologically, it is associated with the Acheulean industry (Mode 2) and is likely to have hunted and potentially cooked its food. Its relationship to later hominins is controversial. *H. heidelbergensis* is known from Africa and Eurasia and is sometimes divided into geographical lineages (*H. heidelbergensis* and *H. rhodesiensis*). Whether they are a single species or two, *H. heidelbergensis* represents the core Middle Pleistocene lineage, widespread across the Old World and ancestral in some way to the later hominin lineages in Africa and Eurasia; namely, modern humans and Neanderthals.

Later *Homo* Diversity

Late Pleistocene species and their evolutionary relationships are relatively well understood, no

doubt because they are better well represented in the fossil record, and more significantly because they existed recently enough for ancient DNA to be preserved. There are three lineages of later Pleistocene hominin currently recognized – Neanderthals, Denisovans, and *Homo sapiens*. The first two are Eurasian, the last African, and all evolved in the last ~300 ky or more.

The Neanderthals are the best-known extinct hominin, and past misconceptions unfairly characterized them in Hobbesian terms as “nasty, brutish, and short.” Relatively short they might have been – they were stockily built, with males averaging 166 cm and females 154 cm – but the archaeological record associated with them suggests they were capable of behaviors that are very similar to those of modern humans. Key questions about Neanderthals concern the degree of behavioral complexity they were capable of and the nature of their distinct morphological features. Anatomically, Neanderthals appear particularly well-adapted to cold Pleistocene European climates: their limb proportions appear to conform to Allen’s Rule (cold-adapted species tend to have short limbs), and their shape and relative robusticity conforms to Bergmann’s Rule (bodies tend to be rounder in colder climates). Neanderthal facial features have also been explained with reference to climate: for example, their relatively large sinuses could have been useful for warming inhaled air. However, this explanation has been challenged, and the distinctive Neanderthal morphology might simply be the consequence of genetic drift in an isolated population.

Neanderthals made standardized stone tools, but this is where consensus about their behavioral repertoire ends. Broadly speaking, there are two major positions: one contends they lacked behavioral flexibility, did not have language, did not bury their dead, did not use fire, and scavenged rather than hunted, and the other suggests the opposite. Current evidence best supports a mild version of the latter. Neanderthal genomes contain the human version of the speech-related FOXP2 gene, and the Kebara Neanderthal hyoid bone shows features consistent with a capacity for speech – although these features do not

necessarily imply “modern” language. Archaeological evidence suggests at proficient hunting: the oldest known wooden spears in Europe date to 300 kya, and lithic spear points date as far back as 185 kya. Claims for advanced “cultural” capacities have been based primarily on the French Châtelperronian industry, which included ivory rings, grooved and perforated animal teeth, and other potential ornaments, but this has been contested on the basis of likely stratigraphic mixing (Higham et al. 2010). It appears Neanderthals used bird feathers, perhaps for decorative purposes. Controversial archaeological evidence aside, their large brains and similar encephalization quotient to humans make it unlikely Neanderthals were incapable of at least *some* “advanced” behavior.

The Neanderthals were not the only Eurasian hominin lineage. The “Denisovans” were first introduced to the paleoanthropological lexicon by Reich and colleagues in 2010, following the successful sequencing of ancient mitochondrial and nuclear DNA extracted from a distal manual phalanx found in southern Siberia. Based on the aDNA evidence, which suggested the individual belonged to a sister group of Neanderthals, the group was named Denisovans after the cave in which their remains were found. So far, they are represented by very fragmented and undiagnostic anatomical elements, and so their phenotype is unknown, but they may have been widespread over large parts of East Asia. When both are compared to modern human genomes, the Denisovan has an unexpected excess of divergent regions in comparison with its Neanderthal sister species, leading Prüfer and others (2014) to propose that these regions could have been contributed by an as yet unidentified species. Alternatively, the similarity between Neanderthals and modern humans might be the result of gene flow from AMHs into Neanderthals, and this is a more parsimonious explanation (Posth et al. 2017).

The Evolution of Modern Humans

It is now almost universally accepted that while Neanderthals and Denisovans evolved in Eurasia, *Homo sapiens*’ roots lie in Africa. This is known

as the “Out of Africa” model, in which AMHs are a distinct African species that replaced existing Eurasian hominins as it dispersed out of Africa around 50 kya. Earlier models proposed a more widespread evolution of modern human traits, with regional continuity from archaic to modern forms, rather than dispersals and replacement. Genetic studies have formed the basis for the Out of Africa model.

Genetic Evidence

The coalescence date of the modern human and Neanderthal lineages gives a lower bound for our species’ independent genetic history. Prüfer et al. (2014) suggest a date of 553–589 kya based on two Neanderthal genomes. All lines of genetic evidence point toward an African origin of AMHs. The highest level of mitochondrial DNA diversity is found in Africa, which can be explained as a result of African populations having a longer period of time to accumulate genetic diversity compared to the populations of AMHs that colonized the rest of the world *after* their emergence in Africa. Mitochondrial DNA lineages coalesce ~200 kya (implying their LCA lived around this time), in accordance with fossil evidence. The same goes for the Y chromosome, although it coalesces at ~150 kya (Jobling et al. 2014). The relatively low amount of whole-genome genetic variation worldwide compared with, for example, chimpanzees, is suggestive of a relatively small founding population resulting from a genetic bottleneck associated with the AMH migration out of Africa.

Fossil Evidence

The oldest fossils showing significant *Homo sapiens* traits are found in Africa: in Jebel Irhoud, Morocco (300 kya); Omo, Ethiopia (195 kya); Herto, Ethiopia (160 kya); and Laetoli, Tanzania (120 kya). Some of these are clearly AMH, while others show mixed traits, suggesting a complex population history. Modern humans are characterized by a rounded cranium with a vertical forehead and reduced brow ridges, a small orthognathic face, a chin, and a tall, relatively gracile skeleton. These earliest AMHs are considerably more robust than current forms, and they

exhibit a mix of archaic and modern features concurring with an African origin.

Archaeological Evidence

There is a general association between the evolution of modern humans and the Middle Stone Age in Africa, although it is the case that both archaic forms in Africa and Neanderthals used Mode 3 technologies (see section “[Technology](#)”). The African archaeological record is dramatically understudied compared to its European counterpart, but despite this, more derived traits such as blades, use of ochre, and use of aquatic resources first occur between 280 and 120 kya in Africa, compared to around 50 kya in Eurasia.

A historically contentious concept is “behavioral modernity.” On the one hand, some scholars have argued the archaeological record is indicative of a mismatch between anatomical modernity and behavioral modernity. The most extreme variety of this standpoint is a “human revolution” where modern human culture, linguistic ability, and cognition suddenly appear at 50 kya, 150,000 years after the emergence of morphologically modern humans (e.g., Mithen 1998). On the other hand, Mcbrearty and Brooks (2000) and others suggest there was a slow, sporadic development of modern human cognition in Africa over a period spanning at least 300,000 years; so, behavioral modernity evolved in tandem with its biological correlates (i.e., large brains and the modern human form). Current evidence supports the latter view, with increasing evidence for unambiguously symbolic behavior as early as 100 kya, and modern human cognition generally, as manifested in various technologies and subsistence behaviors, at ~250 kya (for a full discussion (McBrearty and Brooks 2000)).

Admixture Between Modern Humans and Archaic Hominins

Interbreeding between Late Pleistocene hominins appears to have been a common occurrence. At current count, there is genetic evidence for three to five cases between four distinct populations (Prüfer et al. 2014): between modern humans and Neanderthals, modern humans and Denisovans, Neanderthals and Denisovans, and

Hominin Evolution, Table 3 *Homo sapiens* geographic dispersals. Data from Jobling et al. (2014)

Continent	Date(s) of dispersal(s)
Australia	First colonized ~50 kya
Asia	First colonized 80–120 kya
Europe	At least 3 independent waves of colonization First colonized ~50 kya
Americas	3 (independent) waves Date of first colonization disputed, but probably between 15 and 20 kya

Denisovans and an unknown hominin. The evidence for interbreeding is debated: it has been shown that ancient population substructure generates highly similar genetic patterns to gene flow, and the two scenarios are difficult to differentiate statistically. If assumptions hold, however, and the genetic patterns are the consequence of gene flow, coding sections of introgressed DNA can provide a clue as to the functional consequences of interbreeding. It looks, for example, like Neanderthals and Denisovans contributed immune system genes to modern Eurasian and Oceanian populations, and altitude adaptations in modern Tibetans have been linked to Denisovan-like DNA (Jobling et al. 2014).

The Evolution of Human Diversity

The observed degree of modern human diversity depends on analytical category: on one end of the scale, sociocultural differences between human groups are vast (although all cultures share universal elements), while at the other, we are biologically relatively homogenous – at least compared to other great ape species. These discrepancies reflect differential rates and transmission of change: genetic evolution is transmitted from one generation to the next and is therefore limited by long human lifespans, while cultural change can occur many times within one lifetime and is transmitted both within *and* between generations. What biological variation does exist between human groups tends to be geographically stratified: that is, it is the consequence of populations' individual genetic histories after dispersals into specific regions (or, in the case of Africa, remaining in a region). Although there is disagreement about exact timings, the history of continents' colonization is summarized in Table 3.

Population-specific traits, whether invisible (molecular) or visible (morphological), tend to be explained first with reference to specific ecological circumstances. Ethnic differences in hemoglobin genes are linked to geographic malaria persistence, and lighter skin has been explained as a response to less intense sunshine in northern latitudes. Other processes, such as genetic drift or sexual selection, may have played an equally significant role: blonde hair, for example, confers no direct evolutionary benefit and has instead been shown to be the likely product of sexual selection.

The Out of Africa model of human evolution emphasizes the genetic homogeneity of humans as a species. Biological differences are thus relatively minor and are the product of differential dispersals, local adaptation, and genetic drift under conditions of isolation. Older models that related major racial divisions in the human population have been abandoned.

The Pattern of Hominin Evolution

Hominin evolution is not just a question of phylogenetic and phenotypic change, but is a pattern of adaptive change in response to changing ecological and selective conditions. The fossil record shows a sequence to these adaptive changes.

Bipedalism

Anatomically, obligate bipedalism is one of the most obvious and fundamental differences between our ape relatives and us. The consensus among paleoanthropologists is that bipedalism is a defining feature of the hominin clade and that adaptations for upright locomotion can be used to

assign putative hominin fossils from 7 to 5 Ma to the lineage (see section “[Hominin Origins](#)”). Accumulating evidence suggests at multiple “versions” of bipedalism in the hominin clade (see section “[Early Hominin Evolution](#)”). A key issue in the analysis of locomotor features is interpreting “primitive” arboreal traits shared with Miocene apes: these could be preserved due to functional relevance *or* be inconsequential vestigial remains that were not selected against. In any case, mosaics of locomotor features in early hominins imply bipedalism need not be monophyletic, meaning it could have evolved several times independently within a rapidly diversifying lineage.

The absence of early chimpanzee fossils complicates reconstruction of the precursor to hominin bipedalism. Suggestions for the ancestral condition have included a knuckle-walking ancestor, an orthograde arboreal clamberer, and pronograde clambering similar to orangutans. It is likely the LCA did not brachiate; the Miocene ape *Proconsul*, which likely belongs to the common ancestry of African apes, shows no adaptations to brachiation.

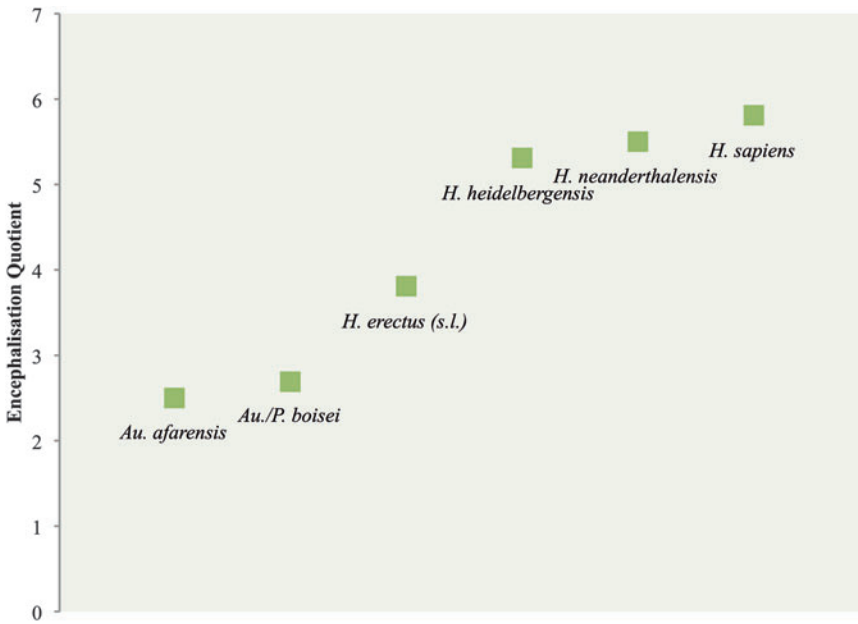
The question of *why* bipedalism evolved remains, and while as many as a dozen explanations have been proposed, they are united in their specific reference to the ecological context within which it did. This context was one of increasing habitat fragmentation. Energetic models suggest bipedalism allows the exploitation of larger areas than the knuckle-walking of modern chimpanzees, with obvious advantages in terms of food acquisition in patchy resource distributions associated with mosaic habitats. Others have suggested a bipedal posture was first habitually adopted in threat displays against predators or as a form of vigilance in increasingly open environments. Thermoregulatory advantages of reducing the surface area exposed to direct sunlight and raising the trunk further from the ground have also been proposed. A further possible advantage of bipedalism was that it freed the hands for carrying, an idea originally proposed by Darwin. These hypotheses are not necessarily mutually exclusive; indeed, it is likely selective pressures associated with changing environments produced

multiple challenges (like increased predation, exposure to heat, and more dispersed resources) to which an upright posture provided evolutionary solutions. And while it provided solutions, bipedalism also engendered energetic costs requiring explanation in comprehensive models of its origins.

Encephalization and Life History

If developing bipedalism is the defining feature of the earlier phase of hominin evolution, encephalization is that of the later phase. Encephalization entails brain growth beyond that *expected* for an animal’s body size and is measured as a ratio of body size to brain size known as the encephalization quotient (EQ). High values imply greater intelligence as they reflect “more” brain than that required to merely coordinate bodily functions. Australopithecine brains stay relatively stable at chimpanzee-like volumes from ~4 to 2 Ma, contrasting with the increase observed in the *Homo* lineage (see Fig. 3). Even within the comparatively encephalized order Primates, *Homo* is exceptionally large-brained, and various adaptive explanations have been proposed to explain the trend (see section “[The Costs of Cognition](#)”). As with the evolution of bipedalism, these causal factors are not mutually exclusive, and it is likely the ultimate selective pressure arose from their interactive effects.

Regardless of their evolutionary advantages, larger brains entail clear energetic costs (see section “[The Costs of Cognition](#)” for a full discussion) for parents and offspring alike. They require a longer period of postpartum growth to reach adult size because the narrow human birth canal, the product of selection for a rounded bipedal pelvis, limits the maximum brain volume attainable in utero. This period of growth creates increased and prolonged energetic demands, met by secondary altriciality – high and prolonged dependence on others, including conspecifics other than parents. The *Homo* “solution” to these demands is a changed life history (the timing of key events in an organism’s life cycle). Human life histories differ from those of African apes in two key ways: they include a long period of childhood after weaning, and women live long after



Hominin Evolution, Fig. 3 Hominin encephalization quotients. Data from Schulkin (2011)

reproductive cessation. By contrast, female apes' physiological systems usually fail together with menopause. These life history shifts appear in tandem with encephalizing brains: analyses of dental and femoral development of fossil hominins have indicated that *Australopithecus* is more similar to African apes in its rate of development, whereas the development schedules of *Homo ergaster* and Neanderthals are more similar to that of *sapiens* (Smith 1994).

Technology

A key difference between extant primates and humans is our extreme reliance on technology for survival – while some primates (chimpanzees and capuchins) do use stones to crack nuts, there is no evidence (yet) of nonhumans purposefully *manufacturing* lithic tools in the wild. Technology is a specific trait within a species' behavioral repertoire, but it is especially ecologically significant as it provides a foundation for other behavioral traits like hunting.

Lithic technology dominates most of human evolution; other raw materials, like bone, antler, and metals, were first used only relatively recently. Hominins have been making stone tools

for at least 3 million years; the earliest simple flaked tools come from Lomekwi in Kenya and are dated to ~3.3 Ma (Harmand et al. 2015). Lithic technology has been classified in several ways reflecting technological, morphological, and stylistic differences, of which the most commonly used are Clarke's (1968) technological modes. He recognizes five modes (see Table 4) which are very loosely arrangeable as a chronological framework cataloguing increasing complexity over time, but with a very strong caveat: the modes overlap considerably, with the "simpler" modes occurring continuously after their first appearance, and the introduction of a novel technology often did not result in the complete replacement of older forms. Obviously, in the frequent absence of hominin fossils associated with lithic assemblages, it is challenging to generalize about species-specific technological abilities. Broadly speaking, however, the earliest simple flaked tools (represented by Mode 1) were manufactured by late australopithecines and early members of *Homo*; Mode 2 bifacially flaked hand axes are frequently associated with *Homo ergaster* and *Homo heidelbergensis*; and prepared core technologies (Modes 3 and 4)

Hominin Evolution, Table 4 Hominin Technology. Adapted from Foley (1987)

Technological mode	African classification	European classification	Characteristics	Distribution
1	Early Stone Age	Lower Paleolithic	Simple, direct percussion producing flakes and chopping tools	From late Pliocene; especially in Africa, but occurs continuously
2			Production of large flakes, extensively retouched; hand axes	Early and middle Pleistocene; extensively in Africa, Europe, and parts of Asia
3	Middle Stone Age	Middle Paleolithic	Systematic preparation of cores prior to striking	Early parts of late Pleistocene in Europe and Africa
4		Upper Paleolithic	Reduced striking platforms with blade production	Late Pleistocene onward; in many parts of the world, especially Europe
5	Later Stone Age	Mesolithic	Microlithic flake and blade production with retouch	Global post-Pleistocene distribution, with some late Pleistocene presence

appear with later forms of *Homo*. Modes 4 and 5 are currently exclusively associated with AMHs. While increasingly complex technological manufacture probably reflects changing cognitive capacities to a great degree, especially in the context of progressively encephalized brains, it should be noted that lithic technology was likely only *one* component of early toolkits and “simple” technology is thus not necessarily synonymous with “simple” cognition. The long stasis of the Asian archaeological record associated with *Homo erectus* (s.l.) has been interpreted this way, for example, but it is highly likely they supplemented their lithic technology with other locally available materials – possibly bamboo. *Homo heidelbergensis* definitely made wooden tools, evidenced by eight throwing spears from Germany dated to ~400 kya. Vegetation-based non-lithic technology was thus within the technological repertoire of species before *Homo sapiens*, but that based on materials such as bone and antler tends to be seen as evidence for increased behavioral complexity and intelligence, mainly because they are found only in association with AMHs.

Culture

Technology is one element, among many, of human culture. “Culture” is commonly seen as the sine qua non of our ecological niche as it is essentially a storage and transmission vehicle for

human behavior. The comparative study of culture in an evolutionary context is an increasingly important field, one example of which is cultural primatology. Paleoanthropologists and cultural primatologists are concerned with, first, *when* and *why* “culture” evolved and second, its biological *consequences*.

The time depth of “culture,” as well as its evolutionary causes, is entirely subject to definition. Cultural primatologists operationally conceive of “culture” as a process, rather than a product: i.e., as information or behavior acquired from conspecifics through some form of social learning. This definition dramatically deposes human culture from its long-held pedestal of exclusivity in one sense, because in this conception culture can be attributed to other modern taxa such as killer whales and chimpanzees. Despite cultural behaviors in nonhumans, human culture remains unique in its scale and complexity, often summarized as the capacity for cumulative culture. The empirical question that follows on from this perspective is, “when did *human-specific* (cumulative) culture appear, and under what selective pressures?” Broadly, two models of cultural emergence prevail: one advocating a “revolution”: a relatively late sudden emergence of culture as a complete “package” associated with the development of language and consciousness (e.g., Mithen 1998). The other posits a gradual

accretion of elements that comprise modern human culture (e.g., Mcbrearty and Brooks 2000). The expanding archaeological record, especially as more evidence in Africa is discovered, tends to support an accretionary pattern, with some elements, potentially including symbolism, appearing before the emergence of AMHs, and others, like blade technology, appearing after. That said, it is true that human culture has markedly increased in complexity over the last ~10,000 years, and this probably reflects an important transition in cultural evolution, and equally that culture probably played relatively little role in the Pliocene and earliest Pleistocene phases of hominin evolution. If a tendency toward cumulative culture is a process that occurred in the last half million years or so, it raises the question of the “cultural status” of different hominins. The limited evidence of the archaeological record would certainly point to marked contrasts between modern humans and, for example, Acheulean-bearing *H. heidelbergensis*, but more subtle differences with Neanderthals, who may have shared considerable cultural complexity with AMHs.

The biological consequences of human culture are significant. By any standard, it is unique in the extent to which it has transformed our surroundings and thus our selective environment. This has contrasting evolutionary effects: on the one hand, it *removes* selective pressures (a culturally constructed environment buffers the genome from “natural” pressures, removing the need to genetically adapt to newly colonized habitats). On the other, it *creates* them, as the constructed environment exerts new evolutionary stresses culminating in gene-culture coevolution. The classic example of this process is lactase persistence in populations with pastoralist ancestry, where individuals in pastoralist communities who continued producing lactase would have been at a nutritional advantage.

Adaptive Radiations

The patterns in hominin evolution can be interpreted as seven adaptive radiations (Foley 2003), where an adaptive radiation is defined as

(rapid) diversification of a group with common ancestry. These radiations are:

- (I) The African apes and earliest hominins in the later Miocene, the products of which are *Sahelanthropus*, *Orrorin*, and *Ardipithecus*.
- (II) The bipedal apes (early australopithecines), whose diversification mainly occurred within mosaics of locomotive features.
- (III) The megadontic specialists (the *Paranthropus* genus): it is unclear whether this was a monophyletic (single ancestor) group or the outcome of a general trend toward megadonty within the Australopithecines and, as such, whether it is a true radiation.
- (IV) The earliest *Homo*: this is the most problematic of the radiations, because the phylogenetic positions of the species within it are precarious (see section “[Hominin Origins](#)”), and it shows relatively little taxonomic diversity or scale of geographical dispersal.
- (V) Pleistocene *Homo*: specifically, *Homo erectus* (s.l.) and its descendants. Underlying this radiation is a major shift in adaptive complex, reflected in changes in morphology and behavior.
- (VI) Larger-brained *Homo*, in the last 0.5 Ma, with the emergence of the Neanderthals, Denisovans, and AMHs.
- (VII) The radiation of *Homo sapiens*, which mostly involved social rather than morphological diversification.

Hominin Diversity

These patterns are, in practice, more continuous, but emphasize the role of diversification and geographical spread in the process of becoming human, rather than the classic *scala naturae* of early reconstructions. The hominin family tree is now speciose, although this is subject to splitting/lumping controversies, where the underlying problem is one of variation – specifically, how much is acceptable between individuals classed as the same species. A splitting perspective would identify about 28 hominin species, and this does not seem unreasonable in the context of modern-

day primate diversity (with approximately 60 genera and 200 species) (Fleagle 1995).

Transitions in Hominin Evolution

An alternative way of making sense of these evolutionary patterns is as a series of transitions (within which adaptive radiations, or other degrees of evolutionary diversification, may have taken place). The question, here, is whether these major changes occur continuously or only during particular periods in prehistory. The distinction between *Homo* and *Australopithecus* is often seen as an important transition, but it is probably more accurate to recognize three major transitions (Foley 2016). They are, in order:

1. Ranging and energetics (~5–4 Ma), with the appearance of habitual bipedalism and changes in ranging behavior as habitats became increasingly fragmented
2. Technology and niche expansion (~3–2 Ma), with the first appearance of lithic technology and animal food processing, as well as features associated with the *Homo* lineage (large brains, reduced dentition, more humanlike body plan)
3. Cognition and cultural processes (~0.5–0 Ma), with the first appearances of “advanced” behavior: depending on definition, this is human seen in humans *or* is common to the Neanderthal and human lineages.

The Evolution of Human Cognition

Evidence for Evolving Cognitive Capacity

Reconstructing the evolution of hominin cognition is fundamentally different to that of other physical features. Thoughts do not fossilize (although their products are occasionally preserved in the archaeological record), but most crucially, the end product – the modern human mind – is more difficult to define than basic anatomy since it is currently not fully understood biochemically nor psychologically. “Cognition” comprises multiple skills and it is possible that these evolved independently, simultaneously, or

in a mosaic fashion; but accurate reconstruction of these patterns is difficult. Broader trends in cognitive evolution, however, are clear: as a whole, hominin cognition evolved increasingly complex functions capable of innovation and abstraction.

This is directly evidenced in increasing brain size, particularly within the *Homo* genus, where both absolute and relative cranial capacities increase exponentially (see Fig. 3). Relative brain size (captured as an allometric relationship between brain and body size in the encephalization quotient [EQ]) is particularly informative about evolving cognition because it suggests “excess” brain presumably used for higher mental processes as opposed to basic functions. Hominin EQs demonstrate a pattern of increasing excess capacity that accelerated during the evolution of *Homo*. This is classically interpreted as evidence of expanding cognitive abilities or intelligence. Beyond broad patterns, elucidating *which* cognitive skills evolved *when* requires finer-grained analysis of where in the brain, specifically, growth occurred. This was long held to be exclusively within the prefrontal cortex, strongly implicating increased social intelligence (Dunbar 1992); but recent reanalyses suggest greater expansion occurred within the cerebellum, implicating fine motor skills (Barton and Venditti 2014).

Evolving cognition is also indirectly captured by its behavioral consequences, which are preserved in the archaeological record. The manufacture of lithic technology is particularly informative because it provides a long and consistent record of change, although other markers of advancing cognition could be used. Two variables – duration of technological tradition and complexity of technology – reflect cognitive states well, but it is important to note that these data are proxies and therefore provide only a scale of the *relative* cognitive abilities of stone tool-producing hominins. Faster turnover of technological traditions and increased complexity within them, manifested in numbers of stone tool “types,” are generally taken as evidence for more advanced cognition; but there are caveats. Stability of tradition is taken as evidence of socially transmitted “culture” in nonhumans, with

associated inferences about advanced cognition; and classifying “complexity” within technocomplexes is subjective. In any case, both variables evidence trends toward advancing cognition over time: technologies change from simple flaked chopping tools to assemblages comprising highly diverse tool types (see section “[Technology](#)”), and there is much faster turnover of later technocomplexes, on average, than earlier ones. Within-species change suggests change was not always in the direction of greater complexity, with later Asian *Homo erectus* (s.l.) displaying fewer technological “types” than earlier African forms – although this might reflect the use of alternative local materials like bamboo. The clearest shift toward complexity in both variables occurs with the emergence of *Homo sapiens*, which produced dramatically more variable and rapidly changing technology than all other hominins.

Crucially, when direct and indirect evidence are analyzed together, it becomes clear that markers of cognitive evolution do not change simultaneously. Encephalization is a universal temporal trend in the *Homo* lineage, but this is not directly translated into equal rates of change in technology. This suggests a complex interaction between encephalization, changes in behavior, and evolutionary processes such as speciation. These patterns demonstrate that elements comprising cognition may have evolved independently. The idea of a sudden emergence of “modern” human cognition as a single, unified package comprising culture, language, and consciousness relatively recently is currently not supported by the evidence, and a more cumulative model is more likely.

Social and Ecological Models for the Evolution of Hominin Cognition

What selective pressures and advantages underlay the observed pattern of hominin cognitive evolution? Various ecological and social answers have been proposed. Clutton-Brock and Harvey (1980) examined the relationship between primate brain sizes and relative home ranges, concluding that larger brains are linked to frugivorous diets and larger home ranges. For hominins, whose diets were likely omnivorous and who became

increasingly specialized for long-distance ranging in fragmented habitats, this link strongly implies a selective role for sophisticated mental processing of large amounts of spatial data. In this view, encephalization was thus primarily ecologically functional.

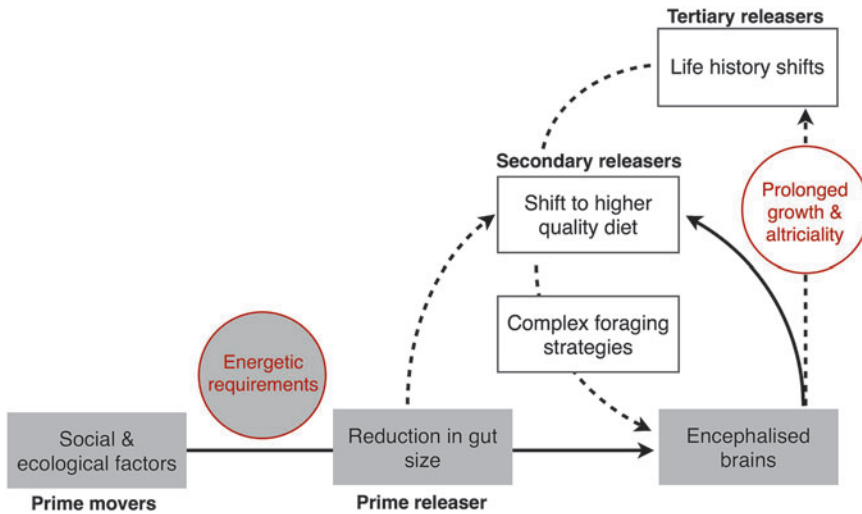
An alternative model is the “social brain hypothesis.” Nicholas Humphrey, Alison Jolly, and Robin Dunbar suggested the problems of living in social environments prompt selection for larger brains. Dunbar (1992) observed a correlation between the relative size of the neocortex and the size of primate social groups. Larger group sizes and associated social complexity thus created selective pressures for bigger, more cognitively advanced brains. This model fits well with the very high levels of social complexity and activity found among humans, with a particularly high degree of social cooperation.

Not all encephalization, however, is found in the neocortex. Recently, Barton and Venditti (2014) demonstrated that the cerebellum, which contains four times more neurons per unit of space than the neocortex, underwent rapid increase during hominin evolution. Consequently, humans have larger cerebella relative to neocortices than other extant primates do. In this “sensory-motor hypothesis,” selection for technical intelligence played a more significant role in cognitive evolution than did social or ecological factors.

These factors, of course, need not be mutually exclusive, and there are clearly interactions between social and ecological factors. Group size, for example, is largely determined by availability and distribution of resources, and equally the size and structure of a group can affect how resources are acquired – for example, hunting among chimpanzees and almost certainly also among hominins.

The Costs of Cognition

Acknowledging evolutionary complexity does not necessarily require the sacrifice of analytical power in favor of untestable description. Falk (1995), for example, does this by making the point that evolutionary models must account for both “prime movers” (major selective agents) and “prime releasers” (changes in physiology that



Hominin Evolution, Fig. 4 A model for the evolution of cognition. *Shaded shapes* represent “primary” factors in this model of cognitive evolution, while *clear shapes* represent secondary and tertiary factors – factors produced as consequences of “primary” factors. *Unbroken arrows* indicate the direction of this evolutionary cause-and-effect.

Circles indicate evolutionary constraints, or costs, mitigated by so-called “releasers” (Falk 1995). Accounting for evolutionary costs involves energetic redistributions or life history shifts to account for tradeoffs between traits, and this process is indicated by *dashed arrows*

relax constraints on traits, thereby permitting their evolution). “Costs,” in the form of evolutionary tradeoffs between traits, are implicit in the concept of prime releasers. Explaining how these costs were physiologically mitigated answers the question of *how* cognition evolved, while prime movers explain *why*. The direct costs of evolving cognitive capacity are increased energetic demands. Aiello and Wheeler (1995) suggested these metabolic costs were met, at the individual level, by a redirection of energy from the gut to the brain, necessitating a reduction in the size of the gastrointestinal tract. Falk categorizes these physiological changes, which *permitted* selection for larger brains, as “prime releasers” (1995). Since gut size is strongly determined by diet, Aiello and Wheeler proposed that this reduction was only possible in the context of a shift to higher-quality diets achieved through more complex foraging strategies – that is, smaller quantities of highly digestible food. These shifts in diet and behavior, then, acted as secondary releasers permitting evolving cognition, and to a degree, they exemplify an evolutionary feedback loop, because complex foraging strategies themselves

necessitate increased intelligence. Encephalizing brains, however, also entail secondary energetic costs met by relatives. Humans have a prolonged postpartum growth period – childhood – necessitated by limitations on maximum brain size attainable in utero due to the narrow human birth canal. In addition, human infants have 9% greater energetic requirements than similarly sized ape infants due to their encephalied brains (Foley et al. 1991). Life history shifts, like the evolution of a long female postmenopausal lifespan, allowed alloparental investment in offspring to account for some of these energetic costs (Hawkes et al. 1998) and thus acted as tertiary releasers (Fig. 4).

The Evolution of Language

The evolution of language is closely related to that of human cognition. Language both *facilitates* cognitive functions (as internal language, or the language of thought) and their *externalization* (speech). Models of language evolution range from an extremely recent, non-Darwinian emergence in *Homo sapiens* alone to extreme time depth with incremental evolution of its component parts throughout hominin evolution. These

contrasting paradigms reflect both differences in definitions of language and the paucity of direct evidence.

Elucidating the evolution of human internal language falls far out of the traditional reach of paleoanthropology (although ingenious attempts have been made), but genetic and anatomical proxies for externalized language suggest at least some form of language in pre-*sapiens* hominins. Neanderthals possessed the derived human version of the speech-related FOXP2 gene (Krause et al. 2007), but its exact role has been debated and its genetic presence alone is insufficient evidence for completely humanlike vocal language. The single Neanderthal hyoid bone from Kebara, Israel, was essentially modern, suggesting a capacity for articulated speech. However, the hyoid provides tentative evidence at best: a modern form is not equivalent to a modern position in the vocal tract. Other attempts to reconstruct speech production by extinct hominins, like analyzing endocast shapes to infer relative sizes of Broca's and Wernicke's areas and linking the size of the thoracic vertebral canal to voluntary control of breathing required for speech, have provided highly ambiguous or statistically unsupported conclusions. "Modern" behavior is linked to both speech and internal language. To the extent that human language is interdependent with symbolic thought, we can infer its existence from "symbolic" artifacts of which the first evidence might extend as far back as shell engravings to 430 kya or a more recent package of evidence for symbolism around the last interglacial (130–70 kya), particularly in Africa. Overall, the evidence suggests language is not the prerogative of modern humans alone; linguistic capacity was likely shared with Neanderthals, also implying a form of language in the LCA they shared. This would place some level of language competence to closer to half a million years ago.

Conclusion

"Our" place in nature is specifically characterized by striding bipedalism; slow life history strategies; large brains capable of complex cognition;

human-specific culture based on abstract, symbolic, and internalized thought with a metacognition; articulated language; and an extreme reliance on technology. These traits are related and interdependent, evolving both in a serial sequence and in parallel, depending on the trait. Fossil, archaeological, and genetic data suggest clear patterns, with bipedalism evolving earlier in human evolution as part of a general shift in ranging and energetics, followed by a technology-based niche expansion. The final period of human evolution was marked by the development of advanced cognition and its behavioral corollaries. However, within each of these phases, there would have been associated coevolution of traits; for example, the coevolution of brain size and changes in life history or diet and technology.

One hundred and 50 years of research into human evolution has revealed much about the tempo and mode of human evolution, showing a complex pattern of novel traits and diversification of lineages, set against a dynamic ecological background. Recent research has been increasingly interdisciplinary, and will continue to be so, with evidence coming from both direct studies of the past – the paleosciences – and inferences from contemporary populations at every level, from the genomic to the cultural.

Cross-References

- ▶ [Ardipithecus Group](#)
- ▶ [Australopithecus africanus](#)
- ▶ [Australopithecus garhi](#)
- ▶ [Australopithecus Group](#)
- ▶ [Brain Evolution Resulting from Cooking](#)
- ▶ [Evolution of Intelligence, The](#)
- ▶ [Extended Postmenopausal Lifespan](#)
- ▶ [Grandmother Hypothesis](#)
- ▶ [Homo habilis](#)
- ▶ [Homo heidelbergensis](#)
- ▶ [Homo neanderthalensis](#)
- ▶ [Homo rudolfensis](#)
- ▶ [Human Tool Making](#)
- ▶ [Linguistic Evolution](#)
- ▶ [Modern Theories of Language](#)
- ▶ [Orrorin tugenensis](#)

- **Paleoanthropology**
- *Paranthropus aethiopicus*
- *Paranthropus boisei*
- **Why Humans Are Unique**

References

- Aiello, L. C., & Wheeler, P. (1995). The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Current Anthropology*, 36(2), 199–221. doi:10.1086/204350.
- Barton, R. A., & Venditti, C. (2014). Rapid evolution of the cerebellum in humans and other great apes. *Current Biology*, 24(20), 2440–2444. <https://doi.org/10.1016/j.cub.2014.08.056>.
- Boyle, E. K., & Wood, B. (2017). Evolution of nervous systems. In J. Kaas (Ed.), (2nd ed., pp. 19–36). Elsevier. Retrieved from <http://www.sciencedirect.com/science/referenceworks/9780128040966#ancv04>.
- Clarke, D. L. (1968). *Analytical archaeology*. Routledge. Schulkin: Front. Evol. Neurosci. Methuen & Co Limited (11 New Fetter Lane London EC4P 4EE). Retrieved from https://books.google.nl/books?hl=en&lr=&id=8BQcBQAAQBAJ&oi=fnd&pg=PP1&dq=clarke+1968+analytical+archaeology&ots=h0ioEfALf8&sig=XbXE1HNdlEXa_rBxHuaY0zjq7oI#v=onepage&q=clarke 1968 analytical archaeology&f=false.
- Clutton-Brock, T. H., & Harvey, P. H. (1980). Primates, brains and ecology. *Journal of Zoology*, 190(3), 309–323. <https://doi.org/10.1111/j.1469-7998.1980.tb01430.x>.
- Dennell, R. W., Rendell, H., & Hailwood, E. (1988). Early tool-making in Asia: Two-million-year-old artefacts in Pakistan. *Antiquity*, 62(234), 98–106. doi:10.1017/S0003598X00073555.
- Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, 22(6), 469–493. [https://doi.org/10.1016/0047-2484\(92\)90081-J](https://doi.org/10.1016/0047-2484(92)90081-J).
- Falk, D. (1995). Comment on: The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Current Anthropology*, 36, 199–221. doi:10.2307/2744104.
- Fleagle, J. G. (1995). Too many species? *Evolutionary Anthropology*, 4(2), 37–38. <https://doi.org/10.1002/evan.1360040202>.
- Foley, R. (1987). *Another unique species: Patterns in human evolutionary ecology*. Longman Scientific & Technical. London: England Mithen
- Foley, R. (2003). Adaptive radiations and dispersals in hominin evolutionary ecology. *Evolutionary Anthropology: Issues, News, and Reviews*, 11(S1), 32–37. <https://doi.org/10.1002/evan.10051>.
- Foley, R. A. (2016). Mosaic evolution and the pattern of transitions in the hominin lineage. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 371(1698), pp 1–14. <http://rsta.royalsocietypublishing.org/content/371/1698/20150244.long>.
- Foley, R. A., Lee, P. C., Widdowson, E. M., Knight, C. D., & Jonxis, J. H. P. (1991). Ecology and energetics of encephalization in hominid evolution [and discussion]. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 334(1270), pp 223–232. Retrieved from <http://rsta.royalsocietypublishing.org/content/334/1270/223>.
- Harmand, S., Lewis, J. E., Feibel, C. S., Lepre, C. J., Prat, S., Lenoble, A., . . . Roche, H. (2015). 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature*, 521(7552), 310–315. [10.1038/nature14464](https://doi.org/10.1038/nature14464).
- Hawkes, K., O'Connell, J. F., Jones, N. G. B., Alvarez, H., & Charnov, E. L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences*, 95(3), 1336–1339. Retrieved from <http://www.pnas.org/content/95/3/1336.abstract>.
- Higham, T., Jacobi, R., Julien, M., David, F., Basell, L., Wood, R., . . . Ramsey, C. B. (2010). Chronology of the Grotte du Renne (France) and implications for the context of ornaments and human remains within the Châtelperronian. *Proceedings of the National Academy of Sciences of the United States of America*, 107(47), 20234–9. <https://doi.org/10.1073/pnas.1007963107>.
- Jobling, M., Hollox, E., Hurles, M., Kivisild, T., & Tyler-Smith, C. (2014). *Human evolutionary genetics* (2nd ed.). New York: Garland Science.
- Klein, R. G. (1999). *The human career: Human biological and cultural origins* (3rd ed.). Chicago: University of Chicago Press.
- Krause, J., Lalueza-Fox, C., Orlando, L., Enard, W., Green, R. E., Burbano, H. A., . . . Pääbo, S. (2007). The derived FOXP2 variant of modern humans was shared with Neandertals. *Current Biology*, 17(21), 1908–1912. <https://doi.org/10.1016/j.cub.2007.10.008>.
- Lordkipanidze, D., Ponce de León, M. S., Margvelashvili, A., Rak, Y., Rightmire, G. P., Vekua, A., & Zollikofer, C. P. E. (2013). A complete skull from Dmanisi, Georgia, and the evolutionary biology of early & homo. *Science*, 342(6156), 326–331. Retrieved from <http://science.sciencemag.org/content/342/6156/326.abstract>.
- McBrearty, S., & Brooks, A. S. (2000). The revolution that wasn't: A new interpretation of the origin of modern human behavior. *Journal of Human Evolution*, 39(5), 453–563. <https://doi.org/10.1006/jhev.2000.0435>.
- Mithen, S. J. (1998). *The prehistory of the mind: A search for the origins of art, religion, and science*. Phoenix.
- Posth, C., Wißing, C., Kitagawa, K., Pagani, L., van Holstein, L., Racimo, F., . . . Krause, J. (2017). Deeply divergent archaic mitochondrial genome provides lower time boundary for African gene flow into Neanderthals. *Nature Communications*, 8, 16046. <https://doi.org/10.1038/ncomms16046>.
- Prüfer, K., Racimo, F., Patterson, N., Jay, F., Sankararaman, S., Sawyer, S., . . . Pääbo, S. (2014). The complete genome sequence of a Neanderthal

- from the Altai Mountains. *Nature*, 505(7481), 43–49. <https://doi.org/10.1038/nature12886>.
- Raichlen, D. A., Gordon, A. D., Harcourt-Smith, W. E. H., Foster, A. D., & Haas, W. R. (2010). Laetoli footprints preserve earliest direct evidence of human-like bipedal biomechanics. *PloS One*, 5(3), e9769. <https://doi.org/10.1371/journal.pone.0009769>.
- Reich, D., Green, R. E., Kircher, M., Krause, J., Patterson, N., Durand, E. Y., . . . Pääbo, S. (2010). Genetic history of an archaic hominin group from Denisova Cave in Siberia. *Nature*, 468(7327), 1053–1060. <https://doi.org/10.1038/nature09710>.
- Richmond, B. G., & Jungers, W. L. (2008). Orrorin tugenensis femoral morphology and the evolution of hominin bipedalism. *Science*, 319(5870), 1662–1665. <https://doi.org/10.1126/science.1154197>.
- Schulkin, J. (2011). Social allostasis: Anticipatory regulation of the internal milieu. *Frontiers in Evolutionary Neuroscience*. Retrieved from <http://journal.frontiersin.org/article/10.3389/fnevo.2010.00111>.
- Smith, B. H. (1994). Patterns of dental development in homo, Australopithecus, pan, and gorilla. *American Journal of Physical Anthropology*, 94(3), 307–325. <https://doi.org/10.1002/ajpa.1330940303>.
- Whiten, A. (2011). The scope of culture in chimpanzees, humans and ancestral apes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 997–1007. <https://doi.org/10.1098/rstb.2010.0334>.
- Wood, B., & Collard, M. (1999). The human genus. *Science*, 284(5411), 65–71. doi:10.1126/science.284.5411.65.
- Zipfel, B., DeSilva, J. M., Kidd, R. S., Carlson, K. J., Churchill, S. E., & Berger, L. R. (2011). The foot and ankle of Australopithecus sediba. *Science*, 333(6048), 1417–1420. Retrieved from <http://science.sciencemag.org/content/333/6048/1417.abstract>.