

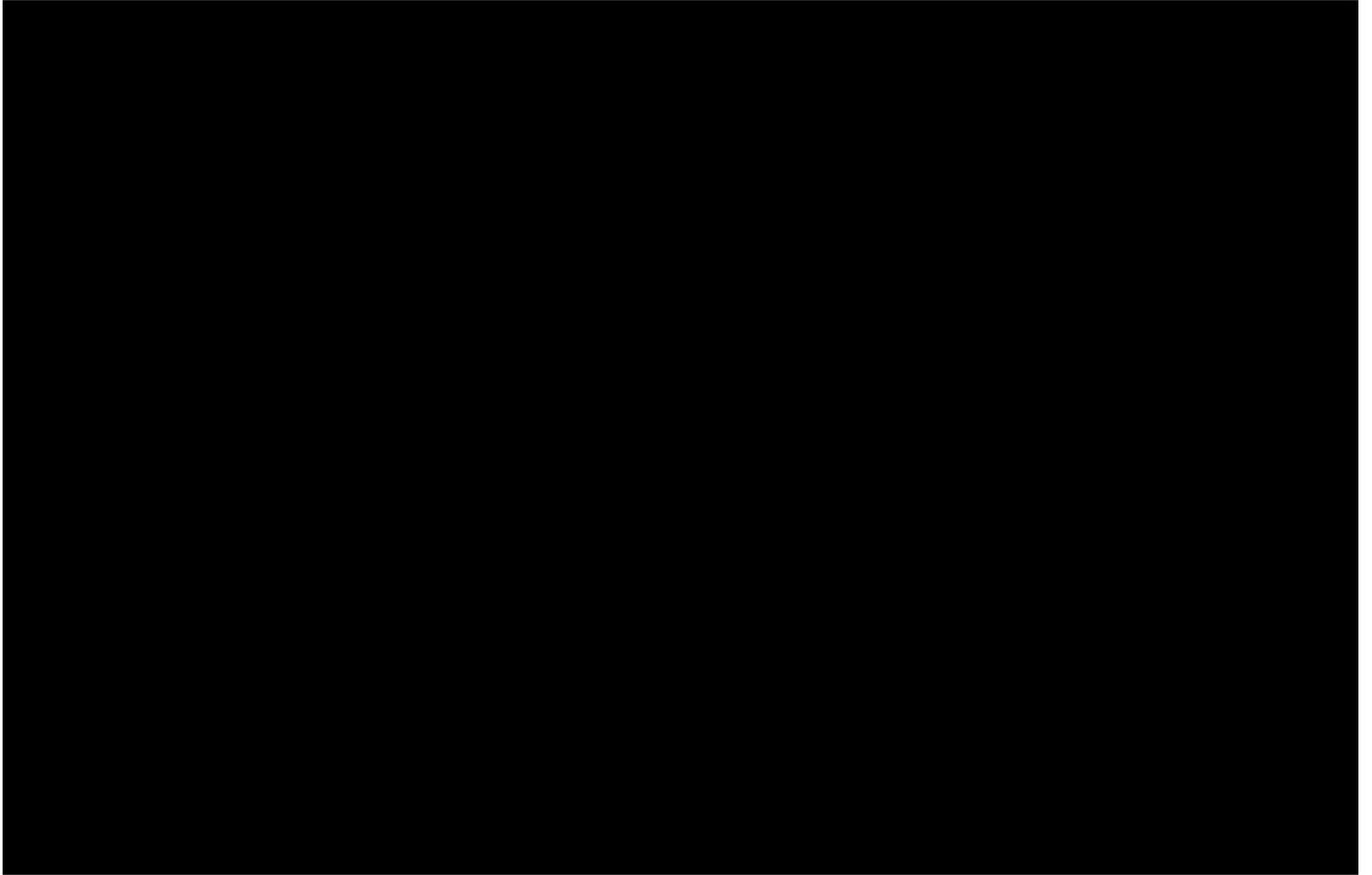


Ardipithecus ramidus and the Paleobiology of Early Hominids

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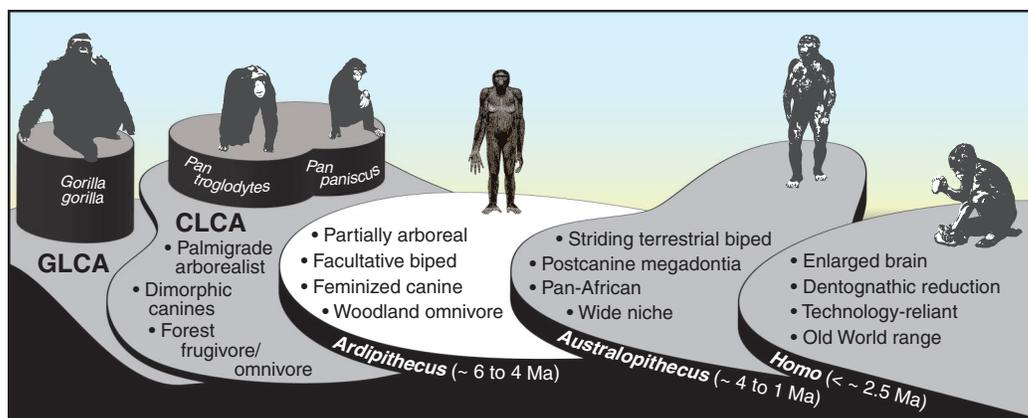
Tim D. White, Berhane Asfaw, Yonas Beyene, Yohannes Haile-Selassie, C. Owen Lovejoy, Gen Suwa, Giday WoldeGabriel

Charles Darwin and Thomas Huxley were forced to ponder human origins and evolution without a relevant fossil record. With only a few Neanderthal fossils available to supplement their limited knowledge of living apes, they speculated about how quintessentially human features such as upright walking, small canines, dexterous hands, and our special intelligence had evolved through natural selection to provide us with our complex way of life. Today we know of early *Homo* from >2.0 million years ago (Ma) and have a record of stone tools and animal butchery that reaches back to 2.6 Ma. These demonstrate just how deeply technology is embedded in our natural history.

Australopithecus, a predecessor of *Homo* that lived about 1 to 4 Ma (see figure), was discovered in South Africa in 1924. Although slow to gain acceptance as a human ancestor, it is now recognized to represent an ancestral group from which *Homo* evolved. Even after the discoveries of the partial skeleton (“Lucy”) and fossilized footprints (Laetoli) of *Au. afarensis*, and other fossils that extended the antiquity of *Australopithecus* to ~3.7 Ma, the hominid fossil record before *Australopithecus* was blank. What connected the small-brained, small-canined, upright-walking *Australopithecus* to the last common ancestor that we shared with chimpanzees some time earlier than 6 Ma?

The 11 papers in this issue, representing the work of a large international team with diverse areas of expertise, describe *Ardipithecus ramidus*, a hominid species dated to 4.4 Ma, and the habitat in which it lived in the Afar Rift region of northeastern Ethiopia. This species, substantially more primitive than *Australopithecus*, resolves many uncertainties about early human evolution, including the nature of the last common ancestor that we shared with the line leading to living chimpanzees and bonobos. The *Ardipithecus* remains were recovered from a sedimentary horizon representing a short span of time (within 100 to 10,000 years). This has enabled us to assess available and preferred habitats for the early hominids by systematic and repeated sampling of the hominid-bearing strata.

By collecting and classifying thousands of vertebrate, invertebrate, and plant fossils, and characterizing the isotopic composition of soil samples and teeth, we have learned that *Ar. ramidus* was a denizen of woodland with small patches of forest. We have also learned that it



Evolution of hominids and African apes since the gorilla/chimp+human (GLCA) and chimp/human (CLCA) last common ancestors. Pedestals on the left show separate lineages leading to the extant apes (gorilla, and chimp and bonobo); text indicates key differences among adaptive plateaus occupied by the three hominid genera.

probably was more omnivorous than chimpanzees (ripe fruit specialists) and likely fed both in trees and on the ground. It apparently consumed only small amounts of open-environment resources, arguing against the idea that an inhabitation of grasslands was the driving force in the origin of upright walking.

Ar. ramidus, first described in 1994 from teeth and jaw fragments, is now represented by 110 specimens, including a partial female skeleton rescued from erosional degradation. This individual weighed about 50 kg and stood about 120 cm tall. In the context of the many other recovered individuals of this species, this suggests little body size difference between males and females. Brain size was as small as in living chimpanzees. The numerous recovered teeth and a largely complete skull show that *Ar. ramidus* had a small face and a reduced canine/premolar complex, indicative of minimal social aggression. Its hands, arms, feet, pelvis, and legs collectively reveal that it moved capably in the trees, supported on its feet and palms (palmigrade clambering), but lacked any characteristics typical of the suspension, vertical climbing, or knuckle-walking of modern gorillas and chimps. Terrestrially, it engaged in a form of bipedality more primitive than that of *Australopithecus*, and it lacked adaptation to “heavy” chewing related to open environments (seen in later *Australopithecus*). *Ar. ramidus* thus indicates that the last common ancestors of humans and African apes were not chimpanzee-like and that both hominids and extant African apes are each highly specialized, but through very different evolutionary pathways.

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Ardipithecus ramidus and the Paleobiology of Early Hominids

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Hominid fossils predating the emergence of *Australopithecus* have been sparse and fragmentary. The evolution of our lineage after the last common ancestor we shared with chimpanzees has therefore remained unclear. *Ardipithecus ramidus*, recovered in ecologically and temporally resolved contexts in Ethiopia's Afar Rift, now illuminates earlier hominid paleobiology and aspects of extant African ape evolution. More than 110 specimens recovered from 4.4-million-year-old sediments include a partial skeleton with much of the skull, hands, feet, limbs, and pelvis. This hominid combined arboreal palmigrade clambering and careful climbing with a form of terrestrial bipedality more primitive than that of *Australopithecus*. *Ar. ramidus* had a reduced canine/premolar complex and a little-derived cranial morphology and consumed a predominantly C₃ plant-based diet (plants using the C₃ photosynthetic pathway). Its ecological habitat appears to have been largely woodland-focused. *Ar. ramidus* lacks any characters typical of suspension, vertical climbing, or knuckle-walking. *Ar. ramidus* indicates that despite the genetic similarities of living humans and chimpanzees, the ancestor we last shared probably differed substantially from any extant African ape. Hominids and extant African apes have each become highly specialized through very different evolutionary pathways. This evidence also illuminates the origins of orthograde, bipedality, ecology, diet, and social behavior in earliest Hominidae and helps to define the basal hominid adaptation, thereby accentuating the derived nature of *Australopithecus*.

In 1871, Charles Darwin concluded that Africa was humanity's most probable birth continent [(1), chapter 7]. Anticipating a skeptical reception of his placement of *Homo sapiens* as a terminal twig on the organic tree, Darwin lamented the mostly missing fossil record of early hominids (2). Following T. H. Huxley, who had hoped that "the fossilized bones of an Ape more anthropoid, or a Man more pithecoïd" might be found by "some unborn paleontologist" [(3), p. 50], Darwin observed, "Nor should it be forgotten that those regions which are the most likely to afford remains connecting man with some extinct ape-like creature, have not as yet been searched by geologists." He warned that without fossil evidence, it was "useless to speculate on this subject" [(1), p. 199].

Darwin and his contemporaries nonetheless sketched a scenario of how an apelike

ancestor might have evolved into humans. That scenario easily accommodated fossil evidence then restricted to European Neandertals and *Dryopithecus* (a Miocene fossil ape). Javanese *Homo erectus* was found in the 1890s, followed by African *Australopithecus* in the 1920s. By the 1960s, successive grades of human evolution were widely recognized. *Australopithecus* comprised several Plio-Pleistocene small-brained species with advanced bipedality. This grade (adaptive plateau) is now widely recognized as foundational to more derived *Homo*.

Molecular studies subsequently and independently confirmed Huxley's anatomically based phylogeny linking African apes and living humans (4). They also challenged age estimates of a human/chimpanzee divergence, once commonly viewed as exceeding 14 million years ago (Ma). The latter estimates were mostly based on erroneous interpretations of dentognathic remains of the Miocene fossil ape *Ramapithecus*, combined with the presumption that extant chimpanzees are adequate proxies for the last common ancestor we shared with them (the CLCA).

The phylogenetic separation of the lineages leading to chimpanzees and humans is now widely thought to have been far more recent. During the 1970s, discovery and definition of *Australopithecus afarensis* at Laetoli and Hadar extended knowledge of hominid biology deep into the Pliocene [to 3.7 Ma (5, 6)]. The slightly earlier (3.9 to 4.2 Ma) chronospecies *Au. anamensis* was subsequently recognized as another small-brained biped with notably large postcanine teeth and postcranial derivations shared with its apparent

daughter species (7, 8). Late Miocene hominid fossils have been recently recovered from Ethiopia, Kenya, and Chad. These have been placed in three genera [*Ardipithecus* (9–12), *Orrorin* (13), and *Sahelanthropus* (14)]. They may represent only one genus (12, 15), and they challenge both savanna- and chimpanzee-based models (16) of hominid origins.

Continuing to build on fossil-free expectations traceable to Darwinian roots, some hold that our last common ancestors with African apes were anatomically and behaviorally chimpanzee-like (17), that extant chimpanzees can be used as "time machines" (18), and/or that unique features of *Gorilla* are merely allometric modifications to accommodate its great body mass. Thus, early *Australopithecus* has routinely been interpreted as "transitional" and/or a "locomotor missing link" (19, 20) between extant humans and chimpanzees. Bipedality is widely suggested to have arisen as an opportunistic, or even necessary, response to a drier climate and the expansion of savannas. These views have been challenged on paleontological and theoretical grounds (9, 21). However, without additional fossil evidence, the evolutionary paths of the various great apes and humans have remained shrouded.

In related papers in this issue (22–27), we describe in detail newly discovered and/or analyzed specimens of *Ar. ramidus*, including two individuals with numerous postcranial elements. All are dated to 4.4 Ma and come from the Middle Awash area of the Ethiopian Afar rift. Local geology and many associated fossils are also described (28–30). These new data jointly establish *Ardipithecus* as a basal hominid adaptive plateau preceding the emergence of *Australopithecus* and its successor, *Homo*. Inferences based on *Ar. ramidus* also facilitate understanding its precursors (22, 23, 27, 31). Here, we provide an integrated view of these studies and summarize their implications.

The Middle Awash. The Middle Awash study area contains a combined thickness of >1 km of Neogene strata. To date, these deposits have yielded eight fossil hominid taxa spanning the Late Miocene to Pleistocene (>6.0 to <0.08 Ma) (32, 33). Hominids make up only 284 of the 18,327 total cataloged vertebrate specimens. Spatially and chronologically centered in this succession, the Central Awash Complex (CAC) (28, 34) rises above the Afar floor as a domelike structure comprising >300 m of radioisotopically and paleomagnetically calibrated, sporadically fossiliferous strata dating between 5.55 and 3.85 Ma. Centered in its stratigraphic column are two prominent and widespread volcanic marker horizons that encapsulate the Lower Aramis Member of the Sagantole Formation (Fig. 1). These, the Gàala ("camel" in Afar language) Vitric Tuff Complex (GATC) and the superimposed Daam Aatu ("baboon" in Afar language) Basaltic Tuff (DABT), have indistinguishable laser fusion ³⁹Ar/⁴⁰Ar dates of 4.4 Ma. Sandwiched between

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Ardipithecus ramidus

the two tuffs are fossiliferous sediments averaging ~3 m in thickness and cropping out discontinuously over an arc-shaped, natural erosional transect of >9 km (28). The rich fossil and geologic data from these units provide a detailed characterization of the Pliocene African landscape inhabited by *Ardipithecus*.

We first surveyed the CAC during 1981 in attempts to understand the distribution of fossils within the region. We launched a systematic program of geological, geochronological, and paleontological investigation in 1992. Initial visits to the CAC's northeastern flank documented abundant fossilized wood and seeds in the interval between the two tuffs. We collected and identified a highly fragmented sample of vertebrates, including abundant cercopithecoid monkeys and tragelaphine bovids. The first hominid fossils were found at Aramis vertebrate paleontology locality 1 (ARA-VP-1) on 17 December 1992. Two initial seasons of stratigraphic and geochronological studies yielded 649 cataloged vertebrates, including a minimum number of 17 hominid individuals represented mostly by teeth (10).

Because of its content, the Lower Aramis Member became the focus of our paleontological

efforts. Fourteen sublocalities within the original ARA-VP-1 locality were circumscribed and subjected to repeated collecting of all biological remains, based on multiple team crawls (35) across the eroding outcrops between 1995 and 2005. Analogous collections were made at adjacent localities (ARA-VP-6, -7, and -17), as well as at the eastern and western exposures of the *Ardipithecus*-bearing sedimentary units (KUS-VP-2 and SAG-VP-7) (KUS, Kuseralee Dora; SAG, Sagantole). The Lower Aramis Member vertebrate assemblage (table S1) now totals >6000 cataloged specimens, including 109 hominid specimens that represent a minimum of 36 individuals. An additional estimated 135,000 recovered fragments of bone and teeth from this stratigraphic interval are cataloged by locality and taxon as pooled "bulk" assemblages. Analogous samples were collected from the Lower Aramis Member on the eastern transect pole (SAG-VP-1, -3, and -6). Fossils from localities higher and lower in the local Middle Awash succession (7, 12, 32) and at nearby Gona (36) are reported elsewhere.

The ARA-VP-6/500 partial hominid skeleton.

Bones of medium and large mammals were usually ravaged by large carnivores, then embedded

in alluvial silty clay of the Lower Aramis Member. Once exposed by erosion, postdepositional destruction of the fossils by decalcification and fracture is typical. As a result, the larger vertebrate assemblage lacks the more complete cranial and postcranial elements typically recovered from other African hominid localities. The identification of larger mammals below the family level is therefore most often accomplished via teeth. The hominid subassemblage does not depart from this general preservational pattern (29).

There was consequently little initial hope that the stratigraphic interval between the two tuffs would yield crucially needed postcranial elements of *Ardipithecus*. The only relevant postcrania (arm elements) had come from slightly higher in the section in 1993 (10). However, on 5 November 1994, Y.H.S. collected two hominid metacarpal fragments (ARA-VP-6/500-001a and b) from the surface of an exposed silty clay ~3 m below the upper tuff (DABT), 54 m to the north of the point that had 10 months earlier yielded the *Ardipithecus* holotype dentition. Sieving produced additional hominid phalanges. The outcrop scrape exposed a hominid phalanx in situ, followed by a femur shaft and nearly complete tibia. Subsequent excavation during 1994

Fig. 1. Geography and stratigraphy of the Aramis region. Two dated volcanic horizons constrain the main *Ardipithecus*-bearing stratigraphic interval in the Aramis region. The top frame shows these tephra in situ near the eastern end of the 9-km outcrop. The dark stripe in the background is the riverine forest of the modern Awash River running from right to left, south to north, through the Middle Awash study area of the Afar Rift. The lower frames are contemporaneous helicopter views over ARA-VP-1 (Yonas Molar Site) to show the geographic position of the top photo and to depict the extensive outcrop of the upper tuff horizon (dotted lines show the DABT) across the local landscape. Vehicles are in the same position to provide orientation. Sediments outcropping immediately below this 4.4-million-year-old horizon yielded the floral, faunal, and isotopic contexts for *Ar. ramidus*. The frame to the left shows the slight eastward dip of the Sagantole Formation toward the modern Awash River. The contiguous frame to the right is a view up the modern upper Aramis catchment. The ARA-VP-6 locality where the partial *Ardipithecus* skeleton was excavated is near its top right corner (Fig. 2).



and the next field season (at a rate of ~ 20 vertical mm/day across ~ 3 m²) revealed >100 additional in situ hominid fragments, including sesamoids (Fig. 2 and table S2). Carnivore damage was absent.

The bony remains of this individual (*ARA-VP-6/500*) (Fig. 3) (37) are off-white in color and very poorly fossilized. Smaller elements (hand and foot bones and teeth) are mostly undistorted, but all larger limb bones are variably crushed. In the field, the fossils were so soft that

they would crumble when touched. They were rescued as follows: Exposure by dental pick, bamboo, and porcupine quill probe was followed by in situ consolidation. We dampened the encasing sediment to prevent desiccation and further disintegration of the fossils during excavation. Each of the subspecimens required multiple coats of consolidant, followed by extraction in plaster and aluminum foil jackets, then additional consolidant before transport to Addis Ababa.

Pieces were assigned number suffixes based on recovery order. Back-dirt was weathered in place and resieved. The 1995 field season yielded facial fragments and a few other elements in northern and eastern extensions of the initial excavation. Further excavation in 1996 exposed no additional remains. Each fragment's position, axial orientation, and dip were logged relative to a datum (strata here dip east at $\sim 4^\circ$ to 5°). A polygon representing the outer perimeter and vertical extent of the hominid fragment constellation (based on each bone's center point) was demarcated by a carapace of limestone blocks cemented with concrete after excavation, then further protected by a superimposed pile of boulders, per local Afar custom.



Fig. 2. The *ARA-VP-6/500* skeletal excavation. Successive zooms on the *ARA-VP-6/500* partial skeleton discovery are shown. Insets show the application of consolidant to the tibia shaft and removal of the os coxae in a plaster jacket in 1994–1995. No skeletal parts were found articulated (the mandible excavation succession shows the close proximity of a proximal hand phalanx and trapezium). Only in situ specimens are shown on the plan and profile views. Note the tight vertical and wider horizontal distributions of the remains. Local strata dip $\sim 5^\circ$ to the east. The lower inside corner of each yellow pin flag marks the center point for each in situ specimen from the 1994–1995 excavation. The 1995–1996 excavation recovered additional, primarily craniodental remains between these flags and the vehicle. The boulder pile emplaced at the end of the 1996–1997 excavation marks the discovery site today.

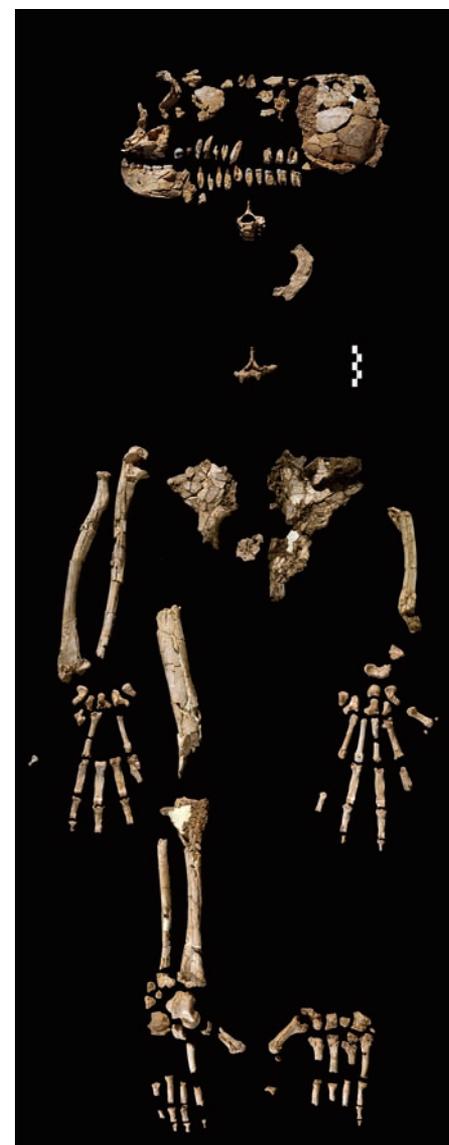


Fig. 3. The *ARA-VP-6/500* skeleton. This is a composite photograph to show the approximate placement of elements recovered. Some pieces found separately in the excavation are rejoined here. Intermediate and terminal phalanges are only provisionally allocated to position and side.

The skeleton was scattered in typical Lower Aramis Member sediment (Fig. 2): fine-grained, massive, unslickensided, reddish-brown alluvial silty clay containing abundant decalcified root casts, fossil wood, and seeds. A 5- to 15-cm lens of poorly sorted sand and gravel lies immediately below the silty clay, and the spread of cranial parts to the north suggests that the bones of the carcass came to rest in a shallow swale on the floodplain.

There is no evidence of weathering or mammalian chewing on *ARA-VP-6/500*. Bony elements were completely disarticulated and lacked anatomical association. Many larger elements showed prefossilization fragmentation, orientation, and scatter suggestive of trampling. The skull was particularly affected, and the facial elements and teeth were widely scattered across the excavated area. Bioturbation tilted some phalanges and metacarpals at high dip angles (Fig. 2). A few postcrania of a large *Aquila* (eagle) and other birds were recovered during excavation, as were a few micromammals. No large-mammal remains (except isolated cercopithecoid teeth and shaft splinters from a medium-to-large mammal limb bone) were associated. The cause of death is indeterminate. The specimen is judged to be female. The only pathology is a partially healed osteolytic lesion suggestive of local infection of the left proximal ray 5 pedal phalanx (*ARA-VP-6/500-044*).

Laboratory exposure and consolidation of the soft, crushed fossils were accomplished under binocular microscope. Acetone was applied with brushes and hypodermic needles to resoften and remove small patches of consolidant-hardened encasing matrix. Microsurgery at the interface between softened matrix and bone proceeded millimeter by submillimeter, rehardening each cleaned surface with consolidant after exposure. This process took several years. The freed specimens remain fragile and soft, but radiographic accessibility is excellent. Most restoration and correction for distortion were accomplished with plaster replicas or micro-computed tomography digital data to preserve the original fossils in their discovery state.

Environmental context. The Lower Aramis Member lacks any evidence of the hydraulic mixing that afflicts many other hominid-bearing assemblages. The unwarranted inference that early hominids occupied “mosaic habitats” (38) is often based on such mixed assemblages, so the resolution and fidelity of the Aramis environmental data sets are valuable. We estimate that the interval of time represented by the strata between the two tuffs at Aramis is $<10^5$ years, and perhaps just a few hundred or thousand years (28, 39). The lithology, thickness, taphonomic evidence, and similar age of the constraining marker horizons imply that geologically, the evidence can be viewed as “habitat time-averaged” (40). Indeed, we do not see notably different environmental indicators in the fossils or geologic or chemical data sampled vertically

throughout the interval. The wealth of data allows a high-fidelity representation [sensu (41)] of the ecological community and environment inhabited by *Ar. ramidus* 4.4 Ma.

A variety of data indicate that the wooded biotope varied laterally across the Pliocene landscape (28–30). The hominid-bearing localities (centered on the *ARA-VP-1* sublocalities) are rich in fossilized wood fragments, seeds, and animal fossils. Here, isotopic paleosol compositions indicate mostly wooded conditions (28). There was obviously more water at Aramis then (4.4 Ma)—supporting a much richer flora and fauna—than there is today. The higher water budget is possibly due to higher elevation during deposition (42) or to paleoclimatic factors such as a more continuous Pliocene El Niño effect (43). An abrupt transition occurs southeast of the *SAG-VP-7* locality, where sedimentary, faunal, taphonomic, and isotopic data imply a more open rift-axial setting depauperate in faunal remains and lacking in primates, micromammals, and macrobotanical remains (29, 30).

Along the northern slope of the CAC, all localities of the Lower Aramis Member yielded tragelaphine bovids, monkeys, and other data indicative of more wooded conditions. Carbon isotopes from the teeth of five *Ardipithecus* individuals found here imply that they fed largely on C_3 plants in woodlands and/or among the small patches of forests in the vicinity. We interpret the combined contextual data to indicate that *Ar. ramidus* preferred a woodland-to-forest habitat (29, 30) rather than open grasslands. This finding is inconsistent with hypotheses positing hominid origins via climate-driven savanna expansion.

Variation and classification. Initial (1994) description of the limited hominid sample from Aramis placed these remains in a newly discovered *Australopithecus* species interpreted as the most primitive then known (10). Subsequent recovery of the *ARA-VP-6/500* skeleton showed that, relative to body size, its dentition was small, unlike *Australopithecus*. Strict cladistic practice required a new genus name for this sister taxon of *Australopithecus*, so the material was renamed as the new genus *Ardipithecus* in 1995, with the lack of megadonty added to the species diagnosis even as the partial skeleton’s excavation was still under way (44). Subsequent discovery of the earlier probable chronospecies *Ar. kadabba* in 1997 (11, 12) was followed by recovery of *Orrorin* in 2000 (13) and *Sahelanthropus* in 2001 (14). These Late Miocene fossils provide additional outgroup material useful in assessing the phylogenetic position of *Ar. ramidus*.

Only two adjacent Ethiopian study areas (the Middle Awash and Gona) have yielded confirmed remains of *Ar. ramidus* to date (7, 36). Neither has produced any evidence to reject a single species lineage as the source of the combined hominid sample from these Pliocene sites. We thus interpret the Lower Aramis Member hominid assemblage as a single taxon (22). Pene-

contemporary (~4.3 to 4.7 Ma) hominid remains from elsewhere are sparse (45, 46), and these are broadly compatible with the now expanded range of variation in *Ar. ramidus* (22, 23). Thus, although continental sampling is still obviously inadequate, describing hominid species diversity in this time frame (47) as “very bushy” seems unwarranted (48).

The amount of variation within the known Afar *Ar. ramidus* sample appears to be lower than typical for species of *Australopithecus*. This is probably due to a lesser degree of sexual dimorphism in *Ardipithecus*, combined with the narrow time window represented by the interval between the two Aramis tuffs. Skeletal dimorphism is notably difficult to assess, except in rare instances of geologically isochronous samples of a species lineage (e.g., A.L. 333 “first family”) (49). For *Ar. ramidus*, the *ARA-VP-6/500* skeleton (Figs. 3 and 4) provides a rare opportunity for guiding a probabilistic approach to sex attribution of conspecific fossils, relying on canines (22) and postcranially based estimates of body size (27). The implication is that there was broad overlap in body size between males and females of *Ar. ramidus*.

Cranial and dental anatomy. The *Ar. ramidus* skull (23) is very similar to the larger, more robust *Sahelanthropus* cranium (*TM 266-01-60-1*) from Chad, also interpreted as an early hominid (14, 50). Some of the differences are probably partly sex-related. *Ar. ramidus* shares with *Sahelanthropus* a small cranial capacity (300 to 350 cc) and considerable midfacial projection but a maxillo-premaxillary complex that is less prognathic than that of modern African apes [not necessarily a derived trait shared with *Homo*, in contrast with (51)]. The *Ardipithecus* and *Sahelanthropus* crania each lack a distinct post-toral sulcus, and both exhibit an anteriorly positioned posterior cranial base.

Most aspects of the craniofacial structure of *Sahelanthropus/Ardipithecus* are probably close to the African ape and hominid ancestral state. Gorilla and chimpanzee cranial morphologies, as well as their specialized dentitions, are clearly divergently derived (22). In *Gorilla*, enhanced facial size and prognathism occur in relation to larger general size and an increasing adaptation to herbivory and folivory. In *Pan* (also with enhanced prognathism), derived cranial form (including anterior basicranial lengthening) probably occurred as a part of enhanced terrestriality accompanied by elevated agonistic behavior and its anatomical correlates, such as tusklike canines (22, 23). The bonobo cranial base and *Ardipithecus* craniofacial structure may be less derived, but even the bonobo seems to be derived in its relatively small face and global dental reduction (22). This was probably at least in part due to decreased intraspecific aggression in the bonobo lineage after separation from the common chimpanzee lineage.

The superoinferiorly short but intermediately prognathic *Ar. ramidus* face lacks the

broadening and anterior migration of the zygomatic area seen to varying degrees in species of *Australopithecus*. The primitive craniofacial pattern shared between *Sahelanthropus* and *Ardipithecus* suggests that the genus *Australopithecus* would later evolve a craniofacial struc-

ture capable of increased postcanine mastication consequent to an ecological breakout from wooded habitats, expanding its foraging into more open environments (7, 10).

The *Ardipithecus* dentition suggests omnivory (22). It exhibits none of the specializations

seen among modern apes; neither the large incisors of *Pongo* or *Pan* nor the specialized molar morphology of *Pongo*, *Pan*, or *Gorilla*. Postcanine size relative to body size was slightly larger than in *Pan* but smaller than in *Gorilla*, *Pongo*, or (especially) *Au. afarensis*. *Ar. ramidus* molars overlap considerably with *Pan* in some measures of enamel thickness but differ in overall thickness and structure. Chimpanzee molars have a broad occlusal basin with locally thin enamel not seen in *Ardipithecus*. *Pan* molar morphology is probably an adaptation to crushing relatively soft and nonabrasive food items such as ripe fruits, while retaining some shearing capacities. The *Ardipithecus* dentition shows no strong signals of ripe-fruit frugivory, folivory-herbivory, or feeding on hard objects. Its macroscopic and microscopic wear patterns, as well as the low bunodont cusps with intermediate enamel thickness (22), suggest that its diet was not particularly abrasive but may have included some hard foods. It is consistent with a partially terrestrial, partially arboreal pattern of feeding in a predominantly wooded habitat.

Carbon isotopic evidence from the teeth of five *Ar. ramidus* individuals suggests that *Ardipithecus* and *Australopithecus* were distinct in dietary intake (30). “Robust” and “nonrobust” *Australopithecus* have enamel isotope values indicating a diet of more than 30% C_4 plants, with variation ranging up to ~80% C_4 . In contrast, the known *Ar. ramidus* individuals vary only between ~10 and 25% C_4 , and thus also differ from *Pan troglodytes*, which prefers ripe fruit and is considered closer to a pure C_3 feeder (30). Thus, *Ardipithecus* appears to have exploited a wider range of woodland resources than do chimpanzees, but without relying on the open biotope foods consumed by later *Australopithecus*.

Evolution of the canine/lower third premolar complex (C/P_3) potentially illuminates social and reproductive behavior. The *Ar. ramidus* canine sample totals 21 Aramis individuals. Some are small fragments, but all show informative morphology and/or wear. All specimens are either morphologically similar to those from female apes or are further derived toward the later hominid condition (22). Morphological and metric variation in the sample is small. Functionally important sex-related size dimorphism is not apparent. There is no evidence of functional honing (planar facets on the mesiobuccal P_3 or sharpened edges on the distolabial upper canine margin). The largest, presumably male, specimens are as morphologically derived as the smallest, showing that dimorphic canine morphology was virtually absent in these hominids by 4.4 Ma. Furthermore, a juvenile probable male lacks the delayed canine eruption seen in chimpanzees, approximating the *Au. anamensis* and *Au. afarensis* conditions and indicating that the canine was not an important component of adult sociobehavioral relationships.

The differential status of upper versus lower canine morphology is informative. In *Ar. ramidus*,

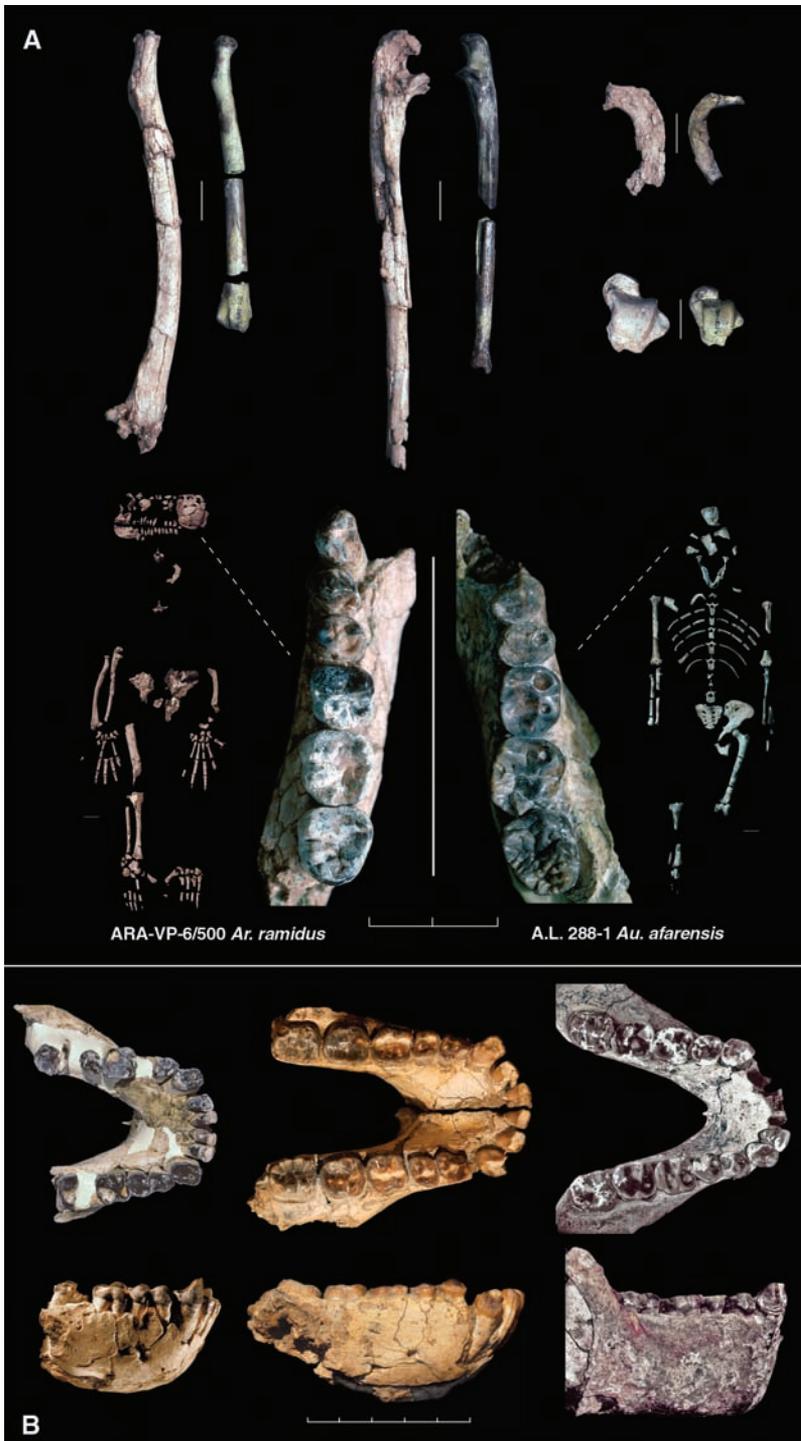


Fig. 4. Comparisons of *Ardipithecus* (left) and early *Australopithecus* (right). (A) Ulnar, radial, first rib, and talar comparisons of the *Ar. ramidus* ARA-VP-6/500 and *Au. afarensis* A.L. 288-1 (“Lucy”) skeletal individuals illustrate larger postcranial dimensions for the *Ardipithecus* individual relative to dental size. Comparison of the postcanine dentitions reveals the megadontia of the *Australopithecus* individual. (B) Occlusal and lateral views of three time-successive mandibles dated to 4.4, 4.12, and 3.4 Ma, respectively, from left to right: ARA-VP-1/401 *Ar. ramidus*; KNM-KP 29281 *Au. anamensis* holotype (mirrored); MAK-VP-1/12 *Au. afarensis* (mirrored).

the lower canines retain modally more ape-like morphology than do the uppers, and, in contrast to other anthropoids, the height of the maxillary canine crown is lower than that of the mandibular (22). This relationship is opposite that seen in great apes and cercopithecids, whose upper canine dominance is exaggerated, particularly in males of dimorphic species. In these primates, upper canine projection and prominence function in both weaponry and display. The *Ar. ramidus* canines are metrically and morphologically derived in the direction of later hominids, and we hypothesize that reduction and alteration of upper canine size and shape in this and earlier hominid species are related to changes in social behaviors (22, 31).

The canines of *Sahelanthropus*, *Orrorin*, and *Ar. kadabba* are broadly equivalent to those of *Ar. ramidus* in size and function. However, the upper canines of Late Miocene hominids exhibit a subtle but distinctly more primitive morphology than their *Ar. ramidus* homologs, potentially including occasional residual (female ape-like) honing as part of their variation (12, 15). This suggests that upper canine prominence was reduced through the Late Miocene and Early Pliocene. In contrast, the C/P_3 complex of the last common ancestor of hominids and chimpanzees probably had a moderate level of canine dimorphism combined with functional honing. This was subsequently generally retained in *P. paniscus* and enhanced in *P. troglodytes*.

Body size and dimorphism. The partial skeleton *ARA-VP-6/500* is identified as female based on probability assessments of canine size (its canines are among the smallest of those of 21 available individuals) (22). This interpretation is corroborated by its small endo- and exocranial size, as well as its superoinferiorly thin supra-orbital torus (23). Bipedal standing body height for the *ARA-VP-6/500* individual is estimated at approximately 120 cm, and body mass at ~50 kg (27). Although actual body mass may vary considerably in relation to skeletal size, this is a large female body mass.

Of the *Ar. ramidus* postcranial elements, the humerus represents the largest minimum number of individuals (seven). *ARA-VP-6/500* does not preserve a humerus, but detailed comparisons suggest that its forelimb was ~2 to 8% larger in linear dimensions than the partial forelimb skeleton *ARA-VP-7/2* (24, 27), which does include a humerus. This would make *ARA-VP-6/500* either the second- or third-largest of eight individuals within the Aramis humeral sample. The combined evidence suggests that *Ardipithecus* skeletal body size was nearly monomorphic, and less dimorphic than *Australopithecus*, as estimated from template bootstrapping (49). Most likely, *Ardipithecus* exhibited minimal skeletal body size dimorphism, similar to *Pan*, consistent with a male-bonded social system, most likely a primitive retention from the CLCA condition (31). With its subsequent commitment to terrestrial bipedality, *Australopithecus* probably enhanced

female cooperation and group cohesion, thus potentially reducing female body size, whereas male size increased in response to predation pressure, probably elevated by expanding niche breadth.

Postcranial biology and locomotion. Regardless of whether the Afar *Ar. ramidus* population represents a hominid relict or a lineal ancestor, this taxon's biology resolves fundamental evolutionary questions persisting since Darwin. Its substantially primitive postcranial anatomy appears to signal a grade-based difference from later *Australopithecus*. The challenge of understanding its evolutionary and functional implications required a nontraditional approach. Without testable hypotheses of underlying gene-based developmental mechanisms, many paleo-anthropological analyses have been adaptationist (52) and/or purely numerically discriminatory. Therefore, wherever possible, in the accompanying postcranial papers (24–27) we restrict hypotheses to those that can be formulated consistent with putative selection acting on cascades of modular-based positional information, especially when these can be potentially grounded in known anabolic mechanisms. This approach is summarized elsewhere (53, 54) and in supporting online material text S1.

The upper pelvis of *Ar. ramidus* presents a contrast to its primitive hand, foot, and limbs. The ilia are abbreviated superoinferiorly and sagittally oriented but broad mediolaterally, so much so that the anterior inferior iliac spine has become a separate growth site, as in all later hominids. The pubic symphyseal face is quite short. A slight sciatic notch is present, although ischial structure was similar to that of extant African apes. This suggests that pattern-formation shifts for bipedality were only partly realized in *Ar. ramidus*. These changes may have culminated a long period of facultative bipedality hinted at by isolated postcranial elements from the probable chronospecies *Ar. kadabba* (12) and other Late Miocene forms (13, 14).

Paramount among the retained primitive characters of the *Ar. ramidus* hindlimb is a fully abductable first ray (hallux, or great toe), but in combination with elements of a robust plantar substructure that stabilized the foot during heel- and toe-off. Although it was still a highly effective grasping organ, the foot of *Ar. ramidus* also maintained propulsive capacity long since abandoned by extant great apes (in which greater opposition between the hallux and lateral rays evolved, i.e., a more handlike conformation than in *Ar. ramidus*) (26).

Other defining and notably primitive characters include a moderately elongate mid-tarsus, a robust lateral peroneal complex in which muscles of the lateral compartment performed substantial plantarflexion, and a primitive (flexion-resistant) geometric configuration of the lateral metatarsal bases. Thus, the *Ar. ramidus* foot is an amalgam of retained primitive characters as well as traits specialized for habitual

bipedality, such as the expanded second metatarsal base that anchored plantarflexion during heel- and toe-off. Many of the foot's primary adaptations to fulcrumation are probable retentions from the gorilla/chimpanzee/human last common ancestor (GLCA), but these have been eliminated in apes, presumably for vertical climbing.

The *ARA-VP-6/500* radius/tibia ratio is 0.95, as in generalized above-branch quadrupeds such as macaques and *Proconsul* (an Early Miocene ape) (27). Its intermembral index (the ratio of forelimb length to hindlimb length) is also similar to those of above-branch quadrupeds. These facts suggest that African apes experienced both forelimb elongation and hindlimb reduction, whereas hominid proportions remained largely unchanged until the dramatic forearm shortening and hindlimb elongation of Plio-Pleistocene *Homo*.

These primitive proportions are consistent with virtually all other aspects of the *Ar. ramidus* skeleton. The inferred locomotor pattern combined both terrestrial bipedality and arboreal clambering in which much weight was supported on the palms. The hand phalanges are elongate relative to those of *Proconsul*, but metacarpals (Mc) 2 to 5 remained primitively short and lacked any corpal modeling or adaptations typical of knuckle-walking (24). Moreover, the virtually complete wrist of *ARA-VP-6/500* (lacking only the pisiform) exhibits striking adaptations for midcarpal dorsiflexion (backward deflection of the dorsum of the hand), consistent with a highly advanced form of arboreal palmigrady. In addition, substantial metacarpal-phalangeal dorsiflexion is indicated both by moderate dorsal notching of the Mc2 to -5 heads and by marked palmar displacement of the capitate head. Together these must have permitted dorsiflexion of the wrist and hand to a degree unparalleled in great apes.

The *Ar. ramidus* elbow joint provided full extension but lacks any characters diagnostic of habitual suspension. Ulnar withdrawal was complete and the thumb moderately robust, with indications of a distinct and fully functional flexor pollicis longus tendon. The hamate's hamulus permitted substantial metacarpal motion for opposition against the first ray. The central joint complex (Mc2/Mc3/capitate/trapezoid) exhibits none of the complex angular relationships and marked syndesmosis reinforcement seen in extant apes. Together, these retained primitive characters, unlike their homologs in highly derived African apes, imply that the dominant locomotor pattern of the GLCA was arboreal palmigrady rather than vertical climbing and/or suspension (orthogrady). Another strong inference is that hominids have never knuckle-walked (26).

The extraordinary forelimb of *Ar. ramidus*, in combination with its limb proportions and likely primitive early hominid lumbar column (55), casts new light on the evolution of the lower spine. The traditional interpretation has

been that the lumbar transverse processes became dorsally relocated as the lumbar column reduced in length. The data from *Ar. ramidus* imply that ulnar withdrawal was not a suspensory adaptation but was instead an enhancement of distal forelimb maneuverability that accompanied profound changes in the shoulder. Spinal column invagination appears to have been an integral part of thoracic restructuring to increase shoulder joint laterality, thereby enhancing forelimb mobility for advanced arboreal quadrupedalism, especially careful climbing and bridging. A still primitive deltoid complex in both *Ar. ramidus* and Asian ancestral apes (e.g., *Sivapithecus*) now becomes more understandable. A predominantly Sharpey's fiber deltoid insertion can be viewed as a retention in above-branch quadrupeds that only later became modified for suspension (separately) in extant African and Asian apes.

The adoption of bipedality and its temporal association with progressive canine reduction and loss of functional honing now constitute the principal defining characters of Hominidae. The orthograde positional behaviors of hominids and apes were thus acquired in parallel, generated by early bipedal progression in the former and suspension and vertical climbing in the latter. Overall, *Ar. ramidus* demonstrates that the last common ancestors of humans and African apes were morphologically far more primitive than anticipated, exhibiting numerous characters reminiscent of Middle and Early Miocene hominoids. This reinforces what Huxley appreciated in 1860: "the stock whence two or more species have sprung, need in no respect be intermediate between those species" [(56), p. 568].

***Ardipithecus* and the great apes.** *Ar. ramidus* illuminates several collateral aspects of hominoid evolution. Despite the demise of *Ramapithecus* as a putative hominid ancestor, at least one Eurasian Miocene ape, *Ouranopithecus*, has been suggested as being phyletically related to later African hominids (57), whereas another, *Dryopithecus*, is often considered an alternative sister taxon of the hominid and African ape clade (58). *Ardipithecus* effectively falsifies both hypotheses. *Ar. ramidus* lacks the derived characters of *Ouranopithecus* associated with postcanine enlargement and relative canine reduction while still providing a primitive morphological substrate for the emergence of *Australopithecus*. The new perspective that *Ar. ramidus* offers on hominoid postcranial evolution strongly suggests that *Dryopithecus* acquired forelimb adaptations to suspensory behaviors independently from African apes. *Ar. ramidus* suggests that these Eurasian forms were too derived to have been specially related to either the hominid or extant African ape clades. Moreover, the remarkably primitive postcranium of potential *Pongo* ancestors (e.g., *Sivapithecus*), coupled with what is now evidently widespread homoplasy in extant hominoids, suggests that the *Pongo* clade was established even before the first dispersal events of large-

bodied apes from Africa into Eurasia, shortly after docking of the Afro-Arabian and Eurasian plates at ~18 Ma (59).

An additional implication of *Ar. ramidus* stems from its demonstration that remarkable functional and structural similarities in the postcrania of *Pongo* and the African apes have evolved in parallel, as have those of *Pan* and *Gorilla* (27). Until now, a myriad of characters shared among the extant African apes were presumed to have been present also in ancestral hominids (because they were presumed to have been the ancestral state) (60). However, it now appears that many of these putative shared primitive characteristics have evolved independently. This highlights the alacrity with which similar anatomical structures can emerge, most likely by analogous selection operating on homologous genomes. The same genetic pathways can be repeatedly and independently coopted, resulting in convergent adaptations (61). Recent work on gene expression demonstrates that there are also multiple pathways that can produce similar but independently derived anatomical structures (62).

Work on deep homology shows that parallel evolution "must be considered a fact of life in the phylogenetic history of animals" [(63), p. 822]. This is also seen in more terminal branches; for example, during the past two million years of stickleback fish evolution (64). Such evolvability and parallelism are even suggested for the catarrhine dentition (65). *Ar. ramidus* reveals an excellent example of this phenomenon within the African ape-hominid clade by demonstrating the striking reoccurrence of syndesmotomic fixation of the central joint complexes in hominoid wrists adapted to suspensory locomotion (including not only those of *Pan* and *Gorilla* but also those of *Pongo* and, partially, *Dryopithecus*). Such observations on very different evolutionary scales all caution against indiscriminant reliance on raw character states to assess phylogeny. A consideration of wider patterns of manifestations of such adaptive evolution, not only in character constellations but also in their evolutionary context, may be needed to tease apart homology and homoplasy. A far more complete fossil record will be needed to accomplish such a goal.

Such considerations also bear on current estimates of the antiquity of the divergence between the human and chimpanzee clades. Many such estimates, suggesting striking recency, have become widely accepted because of the presumed homology of human and African ape

morphologies (60). This obtains despite the recognition that broad assumptions about both the regularity of molecular change and the reliability of calibration dates required to establish such rates have strong limitations (66, 67). The homoplasy now demonstrated for hominoids by *Ar. ramidus* provides fair warning with respect to such chronologies, especially those currently used to calibrate other divergence events, including the split times of New and Old World monkeys, hylobatids, and the orangutan. The sparseness of the primate fossil record affecting these estimates is now compounded by the dangers posed by convergences perceived as homologies. Such difficulties are further exacerbated by newly recognized complexities in estimating quantitative degrees of genetic separation (66–68). In effect, there is now no a priori reason to presume that human-chimpanzee split times are especially recent, and the fossil evidence is now fully compatible with older chimpanzee-human divergence dates [7 to 10 Ma (12, 69)] than those currently in vogue (70).

Hominid phylogenetics. The expanded *Ar. ramidus* sample allows more detailed consideration of early hominid phylogenetics. The placement of *Ardipithecus* relative to later hominids can be approached by using modern and Miocene apes as the outgroup. An earlier cladistic study of this kind concluded that *Ar. ramidus* was the sister taxon of all later hominids (71). A more recent assessment of *Ar. ramidus* dental characters came to the same conclusion (7). In these analyses, a suite of derived features and character complexes exclusively aligning *Ar. ramidus* with *Australopithecus* was identified, but these were based on comparatively limited anatomical elements. The *Ar. ramidus* characters reported here, combined with those from Gona (36), allow a more complete analysis that clarifies the relationships among early hominid taxa.

Parsimony-based cladistic analyses are useful in deciphering relationships within the hominid family tree, despite their shortcomings (72, 73). The distribution of characters identified in Table 1 clearly shows that *Ar. ramidus* is derived relative to all known Late Miocene fossils attributed to the hominid clade. The earlier and more primitive probable chronospecies *Ar. kadabba* is found in 5.5- to 5.7-million-year-old deposits a mere 22 km west of Aramis, consistent with local (and perhaps regional) phyletic evolution. Its limited known elements are similar to those of other Late Miocene hominids in Kenya and Chad (12–14).

Table 1. (See pages 82 and 83.) The assembly of shared derived characters among early hominid taxa. Late Miocene and early Pliocene fossils now allow the strong inference of some character states (primitive, in blue) in the last common ancestor shared by chimpanzees and humans. Many other characters (not shown here) of extant apes were once considered primitive but are now shown to be derived and specific to those lineages. Late Miocene fossils from Ethiopia, Kenya, and Chad share some derived characters (in yellow) with all later hominids. The *Ar. ramidus* sample reported here shows a mixture of primitive and derived characters consistent with its phylogenetic and chronological placement. Phylogenetic implications are in Fig. 5. (An Excel version of this table is available in the supporting online material.)

Table 1. The assembly of shared derived characters among early hominid taxa.

Craniomandibular characters	Chimp/human LCA (INFERRED)	<i>Ar. kadabba/Sa. tchadensis/O. tugenensis</i>	<i>Ar. ramidus</i>	<i>Au. anamensis</i>	<i>Au. afarensis</i>
TMJ articular eminence	flat	flat	flat	TMJ with defined eminence	TMJ with defined eminence
Mandibular corpus breadth	indeterminate	mandibular corpus broad	mandibular corpus broad	mandibular corpus broad	mandibular corpus broad
Mental foramen	indeterminate	circum mid-corpus ht	circum mid-corpus ht	circum mid-corpus ht	secondarily lowered
Mandibular lateral prominence	weak	weak	weak	intermediate	lateral prominence developed
Ramus root/extramolar sulcus	root posterior, sulcus narrow	root posterior, sulcus narrow	root posterior, sulcus narrow	intermediate	ramus root anterior and wide
Symphyseal inclination	strong	strong	strong	strong	extramolar sulcus
Basion position	slightly posterior	anterior	anterior	indeterminate	anterior
Cranial base flexion	moderate midsagittal flexion, orbital kyphosis minimal	advanced?	advanced	indeterminate	advanced
Midfacial breadth	not extreme	not extreme	not extreme	indeterminate	midfacial breadth greater
Zygomatic root	zygomatic root c. M1 present	zygomatic root c. M1 indeterminate	zygomatic root c. M1 present	zygomatic root more anterior	zygomatic root more anterior
Incisor/lower canine step	present	present	present	absent	absent
Dental characters					
Sectorial C/P3 shearing	present, strong in males	sometimes present? in reduced expression?	absent	absent	absent
Canine size dimorphism	dimorphic	reduced C size dimorphism	further reduction?	further reduction	further reduction
Female relative canine size	moderate	moderate	moderate	slightly smaller	slightly smaller
Upper canine shape feminization	males unfeminized, higher crowned, modally lower shoulder	male C feminized in shape	male C feminized in shape	male C feminized in shape	male C feminized in shape
<i>shoulder height</i>	females mostly mid to low	mostly mid to low?	mid to high	mid to high	sometimes extremely high
<i>shoulder flare</i>	weak	weak	distinct flare	distinct flare	distinct flare
<i>lingual marginal ridge</i>	weak	intermediate?	fold-like	fold-like	fold-like
<i>main mesial lingual ridge</i>	strong (secondarily weak in <i>Pan</i>)	strong	basally broad	less prominent	more spatulate
<i>crown height</i>	males tall, females moderate	indeterminate	UC height differentially reduced	reduced	reduced
Lower canine shape feminization	males higher crowned, modally low mesial shoulder, weak/ no distal tubercle	feminized	feminized	feminized	feminized
<i>mesial shoulder height</i>	females vary from low to high	varies from low to high	intermediate?	intermediate?	LC with high mesial shoulder
<i>lingual marginal ridge</i>	weak or none	intermediate?	fold-like	fold-like	fold-like
<i>distal crest</i>	usually weak or none	weak	weak	intermediate	distinct
<i>distal tubercle</i>	weak	developed	developed	variable	distal tubercle less distinct merges with distal crest
Canine enamel thickness	thin	thin	thin	intermediate	thicker
Lower third premolar	hones UC	rarely hones, distal UC wear steep	No hone, distal UC steep	horizontal wear more dominant?	horizontal wear more dominant
<i>basal crown size/shape</i>	obliquely elongate	intermediate?	elongation weaker, relatively smaller size	basally expanded and large	tends to be BL broader
<i>height</i>	tall, with MB cervical extension	intermediate?	MB cervical extension weaker	low, squat, weak extension	weaker extension
<i>metaconid</i>	absent or rudimentary	rudimentary	rudimentary	rudimentary	variably developed
<i>transverse crest</i>	tall, near-transverse to posteriorly directed	near-transverse	near-transverse	near-transverse	more clearly transverse
<i>mesial marginal ridge</i>	weak or none	intermediate?	distinct	distinct	tends to form developed anterior fovea
Upper third premolar	not developed, steep anterior face	weak delineation	better defined	better defined	tendency for more horizontal fovea
<i>anterior fovea</i>	weak to moderate	weak to moderate	weak to moderate	weak to moderate	symmetry more frequent
<i>asymmetry</i>					

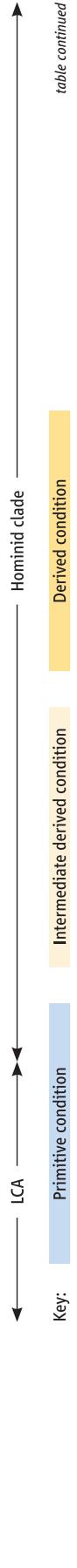


table continued

Table 1. The assembly of shared derived characters among early hominid taxa—continued.

Dental characters (continued)	Chimp/human LCA (INFERRED)	<i>Ar. kadabba/Sa. tchadensis/O. tugenensis</i>	<i>Ar. ramidus</i>	<i>Au. anamensis</i>	<i>Au. afarensis</i>
Lower deciduous molar					
<i>crow shape</i>	buccolingually narrow	indeterminate	buccolingually narrow	intermediate	broad, with developed anterior fovea
<i>protoconid dominance</i>	strong	indeterminate	strong	intermediate	larger metaconid
<i>talonid</i>	little developed	indeterminate	little developed	intermediate	posterior cusps well defined
Molars					
<i>lower molar shape</i>	indeterminate	relatively broader	relatively broader	relatively broader	tends to be very broad
<i>molar row length</i>	moderate	moderate	moderate	size increase	further increase
<i>lower M3 development</i>	variable, usually weak distal crown	variable, usually weak distal crown	variable, usually weak distal crown	large M3 with better developed distal crown	further LM3 complexity
<i>occlusal foveae</i>	moderately broad	moderately broad	moderately broad	narrower (increased basal flare)	narrower (increased basal flare)
<i>crow height</i>	low	low	low	intermediate?	taller M1 crown height
Molar enamel thickness	intermediate, variable	intermediate, variable	intermediate, variable	tends to be thicker	thicker
Canine eruption	males with delayed canine eruption	indeterminate	lacks delayed canine eruption	lacks delayed canine eruption	lacks delayed canine eruption
Premolar to molar wear gradient	slow P3 wear	indeterminate	slow P3 wear	increase of apical P3 wear	increase of apical P3 wear
Postcranial characters	Chimp/human LCA (INFERRED)	<i>Ar. kadabba/Sa. tchadensis/O. tugenensis</i>	<i>Ar. ramidus</i>	<i>Au. anamensis</i>	<i>Au. afarensis</i>
Iliac isthmus	superoinferiorly long	indeterminate	short	indeterminate	short
Pubic symphysis outline	superoinferiorly long	indeterminate	short	indeterminate	short
Ilium/iliac isthmus orientation	coronal	indeterminate	sagittal	indeterminate	sagittal
Iliac breadth	moderately broad	indeterminate	slightly broadened	indeterminate	further broadened with expanded sciatic notch
Anterior inferior iliac spine	not developed	indeterminate	strong, formed by separate ossification center	indeterminate	strong, formed by separate ossification center
Pubic ramus	mediolaterally short	indeterminate	mediolaterally short	indeterminate	elongated
Ischium	long	indeterminate	long	indeterminate	abbreviated
Ischial tuberosity	not angulated	indeterminate	not angulated (INFERRED)	indeterminate	angulated
Greater sciatic notch	not developed	indeterminate	weak	indeterminate	well-developed
Femoral hypotrochanteric fossa	lacks true fossa	lacks true fossa	lacks true fossa	intermediate?	true fossa
Third trochanter and gluteal ridge	strong/rugose 3rd trochanter leading to laterally placed gluteal line	strong/rugose 3rd trochanter leading to laterally placed gluteal line	3rd trochanter weaker but same pattern	3rd trochanter weaker but same pattern	3rd trochanter localized, gluteal line angles medially
Femoral linea aspera	widely spaced med and lat lips	widely spaced med and lat lips	widely spaced med and lat lips	widely spaced med and lat lips	usually true linea aspera
Femoral neck cortical distribution	superior cortex relatively thick	superior cortex relatively thick	indeterminate	indeterminate	superior cortex relatively thin
Hallux	fully abductable, no dorsal doming	indeterminate	fully abductable, no dorsal doming	indeterminate	permanent adduction of hallux, dorsal doming
Second metatarsal	not robust	indeterminate	shaft and base robust	indeterminate	secondary gracilization
Metatarsal heads (rays 2–5)	limited dorsal doming	indeterminate	dorsally domed (Mt3 known)	indeterminate	dorsally domed
Proximal foot phalangeal cant	proximal orientation	indeterminate	upwardly canted	indeterminate	upwardly canted orientation
Trapezoid	mediolaterally narrow	indeterminate	mediolaterally narrow	indeterminate	broader
Capitate	head located palmarly	indeterminate	head located palmarly	head dorsalized and broader	head dorsalized and broader
Metacarpal heads	moderate dorsal constriction	indeterminate	weak, but constriction still seen	indeterminate	constriction lacking
Metacarpal distal end	moderate/strong proximal collateral ligament facets	indeterminate	intermediate?	indeterminate	weak collateral ligament grooves
Skeletal size dimorphism	weak	indeterminate	weak	indeterminate	moderate
Megadontia relative to body size	weak	indeterminate	weak	expressed (INFERRED)	distinct

← LCA

→

← Hominid clade

→

Key: Primitive condition

Intermediate derived condition

Derived condition

Ardipithecus ramidus

Comparatively few features of *Ar. ramidus* are derived relative to these earlier hominids, although many body parts of the latter are still unrepresented. There are no apparent features sufficiently unique to warrant the exclusion of *Ar.*

ramidus as being ancestral to *Australopithecus* (74), and a greatly expanded set of shared derived characters now links *Ar. ramidus* with later members of the hominid clade. Table 1 identifies some of the most important. This pattern robustly falsi-

fies earlier assessments that the Aramis fossils represent an ancestral chimpanzee (13, 75). These results are suggestive of a cohesive hominid evolutionary grade preceding *Australopithecus* (currently >6.0 to 4.2 Ma). By priority, the name *Ardipithecus* may encompass other named genera at this adaptive plateau (12, 15).

The question of whether *Ar. ramidus* is ancestral to later hominids is moot for some cladists because they consider ancestors inherently unrecognizable and therefore recognize only sister taxa (76). The fossils reported here make it even more obvious that *Ar. ramidus* is the cladistic sister to *Australopithecus*/Homo because it shares primitive characters with earlier hominids and apes but at the same time exhibits many important derived characters that are shared exclusively only with later hominids (Table 1).

Species-level phylogenetics are more difficult to discern given the sparse geographic and temporal distribution of available fossils (Fig. 5). Primitive characters seen in *Ar. ramidus* persist most markedly in its apparent (but still poorly sampled) sister species *Au. anamensis* and, to a lesser degree, in *Au. afarensis*. The known dental and mandibular remains of *Au. anamensis* are temporally and morphologically intermediate between those of *Ar. ramidus* and *Au. afarensis*, with variation that overlaps in both directions. Its constellation of primitive and derived features of the mandible, CP₃ complex, lower dm₁ (lower first deciduous molar), and postcanine dentition lends support to the hypothesis of an evolutionary sequence of *Ar. ramidus* → *Au. anamensis* → *Au. afarensis* (7, 8, 77). Circumstantial evidence supporting this hypothesis is the temporal and geographic position of *Ar. ramidus* directly below the first known appearance of *Au. anamensis* within the Middle Awash succession. Here, these taxa are stratigraphically superimposed in the same succession, separated by ~80 vertical meters representing ~200,000 to 300,000 years (7). *Au. afarensis* appears later in the same sequence [3.4 Ma, at Maka (53)].

Therefore, at one end of a spectrum of phylogenetic possibilities, *Ar. ramidus* may have been directly ancestral to the more derived chronospecies pair *Au. anamensis* → *Au. afarensis* across the full (still unknown, presumably African) species range (7, 8, 77) (Fig. 5A). Although *Au. afarensis* is well represented in craniodental remains and postcrania, its apparent earlier chronospecies *Au. anamensis* is still woefully underrepresented in both, and because *Ar. ramidus* is so far known only from limited time horizons and locations, its last appearance, date, and potential relationship to these later taxa are still indeterminate. Given the dramatic differences in postcranial anatomy seen in later *Australopithecus* and hinted at in known *Au. anamensis*, it seems likely that a major adaptive shift marked the *Ardipithecus*-to-*Australopithecus* transition (whenever and wherever the transition might have occurred and whatever its population dynamics). This transition may not have occurred through

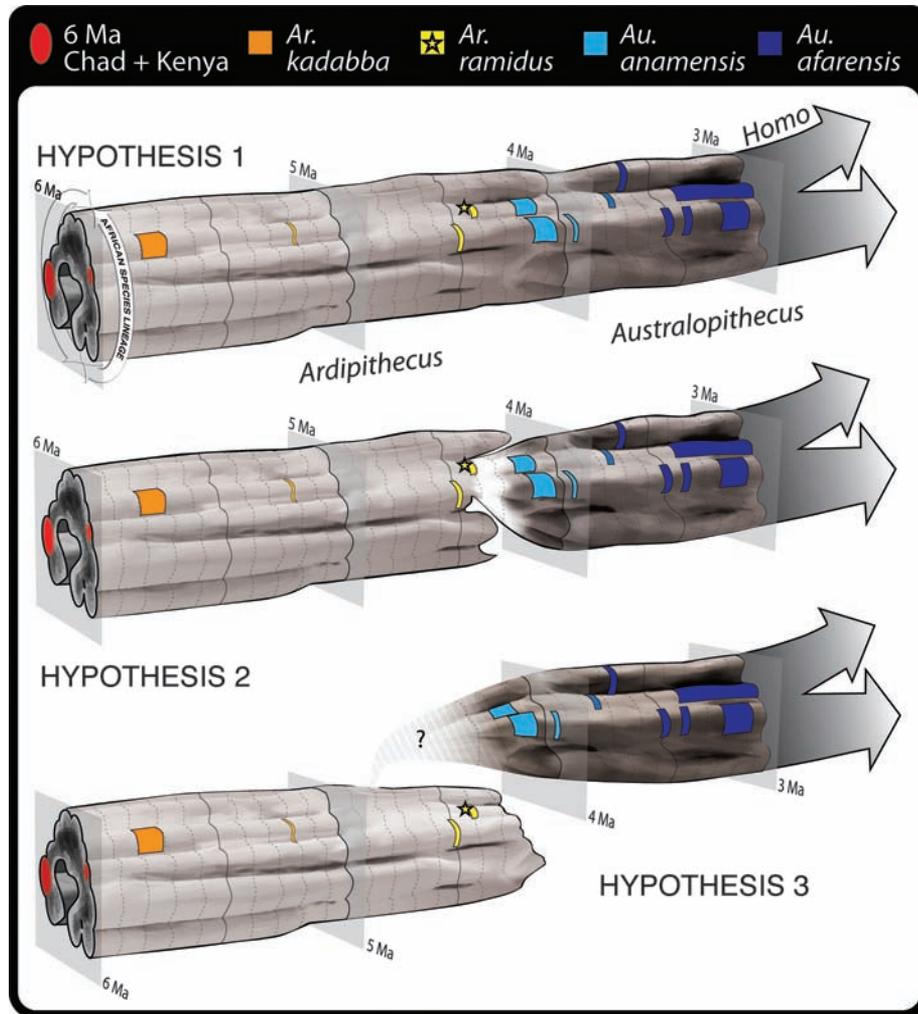


Fig. 5. Geographic and temporal sparsity of early hominid fossils. Colored windows represent presently available samples. Specific and subspecific relationships are currently impossible to resolve because of limited available data. Depicted species lineages are gray “bundles” that comprise sampled and hypothetical subspecific (populational; demic) “cords,” each with continuity through time and reticulating with adjacent populations through gene flow. The slice at ~6 Ma reveals the two known (red) samples of Late Miocene hominids (Chad and Kenya), schematized here for simplicity within the same bundle, pending additional evidence (12). *Au. afarensis* is (so far) sampled in the Ethiopian, Kenyan, Tanzanian, and Chadian (hidden behind the bundle) regions. The Ethiopian Afar region has yielded four named, time-successive taxa, including *Ar. ramidus* (yellow star). The close chronological and geographic proximity of *Ar. ramidus* and *Au. anamensis* within the Middle Awash stratigraphic succession can be accommodated in different stratophenetic arrangements, each with different predictions about future fossil discoveries. Hypothesis 1 interprets all known evidence to represent a species lineage evolving phyletically across its entire range. Hypothesis 2 depicts the same evidence in an *Ardipithecus*-to-*Australopithecus* transition (speciation) occurring between ~4.5 and ~4.2 Ma in a regional (or local) group of populations that might have included either or both the Afar and Turkana rifts. Hypothesis 3 accommodates the same evidence to an alternative, much earlier peripheral allopatric “rectangular” speciation model (cladogenesis through microevolution accumulated in a peripheral isolate population, becoming reproductively separated). Other possibilities exist, but at the present time, none of these hypotheses can be falsified based on the available evidence. To choose among them will require more fossil evidence, including well-documented transitions in multiple geographic locales. See the text [and (7)] for details.

pan-specific phyletic evolution (Fig. 5A). Figure 5 presents two other phylogenetic hypotheses that are also, at present, impossible to falsify.

If diagnostic contemporary fossils of *Au. anamensis* are someday found in rocks of >4.4 Ma, the hypothesis that the Afar population of *Ar. ramidus* is the phyletic ancestor of *Au. anamensis* (Fig. 5A, B) would be falsified. In such an eventuality, Aramis *Ar. ramidus* would represent a persisting relict population of the mother species (Fig. 5C). Given the lack of relevant fossils, it is currently impossible to determine whether there was a geologically rapid phyletic transition between *Ardipithecus* and *Australopithecus* in the Middle Awash or elsewhere. Nevertheless, the morphological and ecological transition between these two adaptive plateaus is now discernible.

***Ardipithecus* and *Australopithecus*.** For Darwin and Huxley, the basic order in which human anatomies, physiologies, and behaviors were assembled through time was unknown—indeed unknowable—without an adequate fossil record. They were forced to employ extant ape proxies instead. The latter are now shown to be derived in ways unrelated to the evolution of hominids.

The Aramis fossils help clarify the origin of the hominid clade (27, 31), and reveal some paleobiological dimensions of the first hominid adaptive plateau (*Ardipithecus*). The primitive characters of *Ar. ramidus* simultaneously provide a new perspective on the evolutionary novelties of *Australopithecus*.

Even in the wake of the Aramis and Gona discoveries, the morphological envelopes, phylogenetic relationships, and evolutionary dynamics of early hominid species remain incompletely understood (Fig. 5). However, the paleobiology of *Ar. ramidus*—even when viewed through its geographically and temporally restricted Afar samples—now reveals that the basal hominid adaptive plateau comprised facultatively bipedal primates with small brains, reduced nonhoning canines, unspecialized postcanine dentitions, and arboreally competent limb skeletons. Their ecological niche(s) were probably more restricted—and their geographic distribution(s) possibly smaller and more disjunct—than those of later hominid species and genera.

The derived postcranial elements of *Australopithecus* provide a strong contrast to their more primitive homologs in *Ardipithecus* (78). Relative to the generalized anatomy of the latter, the highly evolved specializations of the foot, ankle, knee, pelvis, wrist, and hand of *Au. afarensis* (79–81) indicate that this species lineage had largely abandoned locomotion in the arboreal canopy (and its resources).

Given the strong selection predicted to have been associated with the emergence of new ranging and feeding patterns in *Australopithecus*, the transition from *Ardipithecus* to *Australopithecus* could have been rapid, and anatomically particularly so in hindlimb structure. The forelimb

(especially the hand) was probably under less intensive selection. It is possible that modification of general cis-regulatory pathways may have generated the striking and novel morphology of the hindlimb, especially the foot, because the autopod seems to be the most morphologically compliant to such mechanisms of modification. The dentognathic shifts could have been more gradational, whatever the mode of phylogenesis.

Homo and *Australopithecus* are the only primates with nongrasping feet, and this particular transformation was probably far-reaching, with consequences for key behavioral constancies in higher primates related to arboreal feeding and nesting. Without stabilizing selection for *Ardipithecus*-like arboreal capacities involving slow and careful climbing, the foot, pelvis, and thigh would have experienced directional selection to optimize bipedal locomotion during prolonged walking (also in more limited running bouts). With expanded ranging and social adaptations associated with terrestrial feeding in increasingly open environments, the transition could have been profound, but probably rapid, and therefore difficult to probe paleontologically.

One possible dynamic of an *Ardipithecus*-to-*Australopithecus* transition would have involved microevolution within a deme or regional group of demes. Being more ecologically flexible, the derived, potentially speciated populations would have undergone rapid range expansion, perhaps even encountering relict *Ardipithecus* populations. Unfortunately, the phylogeographic details remain obscure given the poor spatial and temporal resolution of the current fossil record (Fig. 5). This provides a strong incentive for pursuing that record by actively increasing sampling of sediments from different African basins with dates between ~5 and ~3.5 Ma.

Currently, *Australopithecus* appears relatively abruptly in the fossil record at about 4.2 Ma. Relative to *Ar. ramidus*, available early *Australopithecus* is now revealed to have been highly derived: a committed biped with slightly enlarged brain, a nongrasping arched foot, further derived canines, substantially specialized postcanine teeth with thick molar enamel, and expanded ecological tolerances and geographic ranges. It is widely recognized that this is the adaptive plateau antecedent to *Homo*, which is now definable as the third such major adaptive shift in human evolution. Commitment to the terrestrial ranging behaviors of *Australopithecus* well before the Pleistocene appear to have catalyzed the emergence of what must have been even more highly specialized social and ecological behaviors remarkably elaborated in descendant *Homo*—the ultimate global primate generalist.

Conclusions. Besides hominids, the only apes to escape post-Miocene extinction persist today as relict species, their modern distributions centered in forested refugia. The markedly primitive *Ar. ramidus* indicates that no modern ape is a realistic proxy for characterizing early hominid

evolution—whether social or locomotor—as appreciated by Huxley. Rather, *Ar. ramidus* reveals that the last common ancestor that we share with chimpanzees (CLCA) was probably a palmigrade quadrupedal arboreal climber/clamberer that lacked specializations for suspension, vertical climbing, or knuckle-walking (24–27). It probably retained a generalized incisal/postcanine dentition associated with an omnivorous/frugivorous diet less specialized than that of extant great apes (22, 23). The CLCA probably also combined moderate canine dimorphism with minimal skull and body size dimorphism (22, 23), most likely associated with relatively weak male-male agonism in a male philopatric social system (22, 23, 31).

Ardipithecus reveals the first hominid adaptive plateau after the CLCA. It combined facultative terrestrial bipedality (25, 26) in a woodland habitat (28–30) with retained arboreal capabilities inherited from the CLCA (24–27). This knowledge of *Ar. ramidus* provides us, for the first time, with the paleobiological substrate for the emergence of the subsequent *Australopithecus* and *Homo* adaptive phases of human evolution. Perhaps the most critical single implication of *Ar. ramidus* is its reaffirmation of Darwin's appreciation: Humans did not evolve from chimpanzees but rather through a series of progenitors starting from a distant common ancestor that once occupied the ancient forests of the African Miocene.

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73. For example, it has been noted that these methods fail to accurately resolve relationships of modern hominoid species without sufficient intermediate forms from a fossil record (71).
74. Enamel thickness of *Ar. ramidus* molars ranges largely from what would traditionally be termed “intermediate thin” to “intermediate thick” categories. Lacking the derived thickness pattern of *Pan*, it forms a suitable ancestral condition for later *Australopithecus*. The ubiquitous single-rooted lower fourth premolar (P_4) in known Aramis and Gona *Ar. ramidus* is notable, but this is also a known variation of *Au. anamensis* and *A. afarensis*. Judging from the clear dominance of double-rooted lower P_4 ’s in *Au. afarensis* (and thereafter an increasing robusticity of the roots themselves in *Australopithecus*), either there was selection for larger, more complex premolar root systems or such morphology emerged as pleiotropy of postcanine enhancement.

Without such selection, *Ar. ramidus* as a species probably contained regional populations that varied in premolar root number (22).

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78. We use genera to express both phyletic proximity and circumscribed adaptive systems, with ecobehavioral and morphological conditions being integral parts of the latter. This use employs the broadly defined genus *Australopithecus*, without recognizing the now commonly used *Paranthropus* (82). This is because both “robust” and “nonrobust” *Australopithecus* species are characterized by a commonly derived heavy masticatory apparatus (albeit to differing degrees), and also because we cannot—even to this day—be certain that the “robust” species are monophyletic.
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Supporting Online Material

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