

Early hominins

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- Last time we saw how apes radiated (diversified) in the middle Miocene
 - most of the apes were forest dwellers
 - some shifted from quadrupedal to more “suspensory” way of moving with long arms
- but later in the Miocene, the temperature was dropping rapidly
 - tropical forests were shrinking
 - leaving patches of temperate forest separated by increasingly open grassland
 - as their forest environments shrank, many of Miocene apes went extinct in the Late Miocene
- one of the surviving species of ape responded to these changes in a new way
 - it came down from the trees and became habitually bipedal
 - around the end of the Miocene and the beginning of the Pliocene, between 6 and 5 mya
 - the features that had helped the Miocene apes live in trees also happened to allow for limited bipedalism on the ground
 - much as modern apes (gorillas, chimps, gibbons, etc.) can walk bipedally at times
 - as trees got farther apart and there were more open spaces, natural selection may have favored apes that were better at bipedal walking
- this was the split that led to **hominins**: the bipedal apes
 - a subset of hominoids (apes)
 - other than bipedalism, they weren't very different from other apes, especially at first
 - humans are the only living species of hominins, but there were many more in the past
 - the first thing that distinguished our ancestors from other primates was bipedalism
 - *not* large brains; those came much later
- we have very few fossils from the late Miocene to tell us about the origin of hominins
- but DNA evidence shows that hominins split from the lineages that led to chimps, bonobos, and gorillas around 7 to 5 mya
 - that is, we, chimps, bonobos, and gorillas all descended from one ancestral species of ape that lived near the end of the Miocene, around 7 to 5 mya
- we also can be pretty sure that this transition to bipedalism happened in Africa
 - there were Miocene apes in both Africa and tropical Asia
 - but *all* of the remains of hominins other than our genus *Homo* are from Africa
- First suspected hominin: *Sahelanthropus tchadensis* (7-6 mya) (Late Miocene)
 - about when hominins split from the line that led to chimps
 - some apelike features
 - chimp-sized brain
 - ape-like teeth (large canines, wide incisors, U-shaped dental arcade, etc.)
 - key hominin feature
 - foramen magnum under braincase: upright, bipedal?
 - some features not seen again until much later hominins

- fairly vertical face
- massive browridges
- did these continue directly to the later hominins, or did they evolve separately later?
- the late Miocene ape *Orrorin tugenensis* (6.1 to 5.2 mya)
 - The head of its femur (thigh bone) is large, suggesting that it evolved under selection for durability in a creature that spent a lot of time on its hind legs – a biped
 - if correct, that would make *Orrorin* an early hominin
 - Its humerus (upper arm bone) and one long, curved finger bone suggest it still had some features associated with hanging in trees
 - The environment, as reconstructed from other animal fossils found with it, was open grassland with patches of forest
 - just as expected for an arboreal ape that was becoming a part-time terrestrial biped
- while *Orrorin* was still around, *Ardipithecus ramidus* appeared (5.8 to 4.4 mya)
 - still poorly known, based on teeth and a few larger fragments
 - but: the foramen magnum is more forward, under the head, than in other apes, hinting at habitual upright posture - and thus bipedalism
 - apparently lived in wooded areas
 - based on seeds and other animal fossils found with *Ardipithecus* fossils
- a bit after 5 mya, one genus of hominins appeared and diversified into many species: the genus *Australopithecus* = “southern ape”
 - **australopithecine** refers to members of the genus *Australopithecus* in general, regardless of the species
 - often abbreviated as A., for example *Australopithecus anamensis* = *A. anamensis*
- earliest australopithecine: *Australopithecus anamensis* (around 4.2 to 3.9 mya)
 - mostly known from teeth, but some cranial, mandible, and limb fragments
 - upper and lower jaws and teeth were quite similar to apes - not very hominin-like
 - relatively U-shaped dental arcade (typical of other apes, not hominins)
 - but with some features that became typical of later australopithecines
 - reduced canines
 - relatively enlarged molars
 - thick enamel on the molars, indicating selection for grinding hard seeds
 - knee joint (top of tibia, or shin bone) suggests bipedalism
 - enlarged joint surface to withstand heavier use
 - concave joint surface limits twisting and side-to-side motions
 - ankle joint (bottom of tibia) also limits motion, as in bipeds
 - and elbow joint is like ours, rather than like apes that use arms for support on the ground
 - ape elbows lock in a straight position, the way our knees do
 - human elbows do not
 - and neither did *A. anamensis*'s elbow
 - so it probably did not lean on its arms much - which hints at bipedalism

- We don't know how these early hominins were related, and there were probably many more that we have not yet found fossils of
 - they just give us an impression of the general kinds of bipedal apes that led to later hominins
- Early hominins snap into focus around 4-2.9 mya with *Australopithecus afarensis*
 - the earliest bipeds that we have plentiful evidence of
 - The first discovery was a knee joint, which had details that suggested bipedalism
 - the team of Maurice Taieb and Don Johanson returned the next year to a place called Hadar and found the famous “Lucy”
 - an incredibly complete specimen
 - Lucy, an adult female, was a little over a meter tall (3' 3”), weighed around 60 pounds
 - with clear signs of well-developed bipedal locomotion
 - the next year, they found fossils of 13 more individuals in a single spot
 - the “first family”
 - maybe part or all of a group killed all together by some disaster, like a flash flood
 - additional *A. afarensis* fossils have been found since
 - not only in the original find area (the Afar depression), but also in other parts of Africa
 - so this was a successful, widespread species
 - all lived in environments ranging from a patchy woodland-grassland mix to an open grassland with only occasional trees
 - *A. afarensis* is often described as basically a bipedal chimp with some dental changes
- *A. afarensis* had a mix of ancestral ape traits and some new traits that hinted at humans
 - ancestral traits (shared with other apes)
 - small brain: **cranial capacity** averaged 404 cubic centimeters, similar to a modern chimp
 - cranium was low, with the bottom part wide and chunky (“pneumatized”), like chimps
 - the face below the nose slopes forward (it is **prognathic**), like a modern chimp
 - derived traits (new traits that distinguished *A. afarensis* from other apes)
 - front teeth were generally reduced compared to Miocene apes
 - back teeth (premolars and molars) were larger, as is typical for australopithecines
 - dental arcade (arched arrangement of teeth) is intermediate between the ancestral “U” form of the apes and the human “parabolic” form
 - U form has straight, parallel sides from canines back
 - parabolic form has a smooth curve that continues to flare apart even at the back
 - *A. afarensis* was intermediate between the two
 - reduced canine size
 - *A. afarensis* had canines smaller than the Miocene apes and modern apes like chimps
 - but still larger than humans
 - reduced **diastema**, or space between the upper incisors and canine to leave room for the large lower canine to fit into
 - in Miocene apes and modern non-human apes, there is a large diastema
 - in humans, the canines are so reduced that there is no need for a diastema
 - *A. afarensis* had a small diastema, leaving room for its small lower canine
 - all suggesting less need for big canines

- that is, less need for big canines in fighting, hunting, male-male competition?
- and more need for grinding
 - because having smaller canines allows the jaw to move side to side more freely
 - that is, eating more hard seeds, as produced by grasses?
- but most important: *A. afarensis* was **bipedal**
 - pelvis is shaped for bipedalism
 - flares out above hip joint to give leverage to muscles that attach to outside top of femur
 - knee is angled, which makes it more stable for bipedalism
 - other apes have straight knees
 - humans and *A. afarensis* have angled knees, so the knees can be close to the centerline of the body and can carry the weight straight down, rather than sliding or prying the knee at each step
 - *A. afarensis* may not have been as completely committed to walking as we are
 - some foot bones from South Africa are probably from *A. afarensis*
 - although since this foot was found without any other part of the skeleton, it could be from some other unknown species
 - these show a foot that could walk bipedally, but could still grasp with its big toe
 - suggesting a mixed terrestrial and arboreal adaptation
 - *A. afarensis* hand bones have thin, curving fingers
 - suggesting ape-like hanging function
 - *A. afarensis* scapula (shoulder blade) also looks adapted for hanging by the arms
- Proof positive of a bipedal hominin around 3.5 mya
 - a trait of footprints from Laetoli (Tanzania)
 - found by Mary Leakey and her team
 - a volcano erupted and covered the ground with ash
 - one or two adults and a juvenile walked across the ash just as a light rain fell
 - maybe together, or maybe not at the same time
 - as the ash dried, it hardened and preserved their footprints
 - the prints were clearly made by efficient bipeds, virtually indistinguishable from footprints left by modern small humans
 - that is, not rocking side to side, shuffling, etc.
 - the very same gait as modern humans
- Why did some apes become bipedal?
 - A key question, because bipedalism is what first set our lineage apart from other primates
 - and set up the conditions that led to greater intelligence, tool manufacture, civilization, etc.
 - many ideas, no consensus
 - Efficiency: bipedalism may be the most efficient form of locomotion on the ground for animals that are basically built to hang in trees
 - for an arboreal ape that had to cross open grassland, walking as a poor biped may have been more efficient than walking as an even poorer quadruped
 - so selection might have favored improvements in bipedalism rather than shifting back towards quadrupedalism

- Cooling: in increasingly open grasslands, bipedalism may have helped prevent overheating
 - bipedalism holds the body vertical, instead of horizontal as in quadrupedalism, so...
 - the sun strikes a smaller fraction of the body when it is upright
 - Just compare your sunburn on days you walk around vs. days you lay on the beach
 - standing up gets the upper body away from the ground
 - where air temperature is generally lower
 - and where there is more wind, which helps cool the body
- Freeing the hands to carry things
 - like food from a dangerous place to a tree where it can be eaten safely
 - problem: chimps carry things in their hands fairly well even without being good bipeds
- Standing upright is useful for picking fruit from trees
 - by analogy to modern chimp behavior
- Standing upright might give you a better view over tall grass
- Other features of *A. afarensis*
 - body size is large compared to most other apes, but smaller than humans
 - in arboreal animals, large size limits mobility, feeding, and escaping, so they remain small
 - once hominins left the trees, they could become larger, maybe in defense against predators
 - highly sexually dimorphic
 - based on the “first family” and other finds
 - so probably non-monogamous social groups, with plenty of male-male competition
 - unusual diet for an ape, similar to other australopithecines
 - large molars with thick enamel suggests grinding lots of hard seeds, nuts, etc.
 - no stone tools yet
 - although they may have made perishable or very simple tools like modern chimps do
 - we would not detect this kind of toolmaking if *A. afarensis* had done it
 - such toolmaking would be expected, since otherwise it would have to have evolved twice, separately in the chimp line and the hominins
 - what creature made the footprints?
 - until 2001, most people assumed it was *A. afarensis*
 - *A. afarensis* fossils have been found in the vicinity
 - no other bipedal species was known from this period, 3.5 mya
 - although some experts argued that *A. afarensis* was not built to walk in exactly the way the footprints were made, and held out for another, yet unknown species
 - sure enough, in 2001, a new species was announced that lived at the same time as *A. afarensis*, and might have been bipedal
 - *Kenyanthropus platyops*, around 3.5 mya
 - poorly known yet
 - foramen magnum was under the braincase, so *Kenyanthropus* was probably upright
 - no postcranial bones are known yet, so we can't tell for sure if it was bipedal
 - but now we don't know if some of the postcranial bones found in the area are really *Kenyanthropus*, rather than *A. afarensis*
 - but we know that there was one *fully* bipedal ape around 3.5 mya that made the footprints
 - and probably at least one other bipedal ape running around Africa at the very same time

- Implications of the new species *Kenyanthropus platyops*
 - it is quite different from *A. afarensis* in numerous face, cranial, and dental traits
 - molars are small, not like the huge molars of *A. afarensis*
 - so it lacked the specializations for eating hard nuts or seeds that developed in *A. afarensis*
 - the many differences imply that the lineage that led to *Kenyanthropus* probably split from the one that led to *A. afarensis* long before, so each had time to evolve in different directions
 - we used to think there was a single line of early bipedal apes, represented by *A. afarensis*
 - but now we know of at least two lineages of bipedal apes evolving at the same time
 - with different diets, and probably other differences
 - which lineage (*Australopithecus* or *Kenyanthropus*) led to us, and which went extinct?
 - if australopithecines were our ancestors, they must have evolved their massive grinding teeth and muscles, then lost them again on the way to us
 - but *Kenyanthropus* had small molars, like ours
 - if *Kenyanthropus* was our ancestor, there need not have been the detour through a heavy grinding adaptation
 - but other subtle evidence supports some australopithecine as our ancestor
 - no consensus yet
- Let's look at the next chunk of time: 3.0 – 1.0 mya
 - often called the Plio-pleistocene (end of the Pliocene, beginning of the Pleistocene)
 - numerous species of bipedal apes (hominins), more varied adaptations
 - in some times and places, 2 or 3 hominins lived in the same environment at the same time
 - *Australopithecus* species (australopithecines)
 - presumably descendents of the earlier *A. afarensis* and maybe others
 - at least 4 species during this period
 - up to 2 at the same time
 - *Paranthropus* species (**paranthropines**)
 - at least 3 species during this period
 - up to 2 at the same time
 - plus possible descendents of *Kenyanthropus*, although no fossils have been found yet
 - plus, halfway through this period (1.8 mya), the first species of our genus: *Homo*
 - we'll look at those later
- All the Plio-pleistocene hominins (3.0 to 1.0 mya) shared certain basic features:
 - all bipedal
 - all had similar small bodies, only slightly larger than Lucy (*A. afarensis*)
 - all had chimp-size brains (chimps have a cranial capacity of about 400 cc; gorillas 540 cc)
 - except one late australopithecine that evolved a larger brain
- Plio-pleistocene australopithecines (3.0 to 1.0 mya)
 - all shared the peculiar heavy grinding diet adaptation, probably for hard seeds like grasses
 - large molars (and premolars)
 - reduced canines
 - **zygomatic arches** leave space for large temporal muscles
 - zygomatic arches are sturdy for attaching strong masseter muscles

- fairly prognathic face
- probably several different lineages
- all went extinct, unless one led to humans
- *Australopithecus africanus* (3.0-2.2 mya)
 - both South Africa and East Africa
 - enough fossils known that we can say a bit more about this species than others, such as:
 - continues marked sexual dimorphism in body size
 - even though reduction in canines (to facilitate grinding?) means males no longer have much larger canines than do females
 - short, rapid juvenile development
 - similar to chimps, not humans
 - based on counting daily “rings” in tooth enamel
 - no evidence of tool making
 - famous example: the Taung child
- *Australopithecus garhi* (2.5 mya)
 - recently discovered, still not many fossils
 - basically, just another australopithecine, but a particularly strong chewer
 - larger molars and premolars
 - **sagittal crest**: attachment of big temporal muscles that meet at the top of the head
 - but surprise!: several animal bones found nearby have cutmarks from flaked stone tools!
 - the stone tools themselves were not found
 - but no suitable stone is available near the site
 - so the material or finished tools must have been brought to the site by someone
 - making flaked stone tools and transporting them is beyond anything observed in chimps
 - did *A. garhi* make the tools?
 - if so, *A. garhi* would have been smarter than its brain size suggests
 - if so, it might be a candidate for our ancestor
 - but if so, then the heavy chewing adaptation must have developed in our lineage, then disappeared again
 - or did a descendant of *Kenyanthropus*, yet undiscovered, make the tools?
 - if so, no need to imagine that chewing developed and then declined again in our lineage
 - but we don’t have fossils to show that *Kenyanthropus* left any descendents
 - maybe some other unknown hominin, like still undiscovered ancestors of the bigger-brained, later *A. rudolfensis*?
- *Australopithecus rudolfensis* (2.4-1.6 mya)
 - not too different from other australopithecines
 - short, fast juvenile development, like other australopithecines
 - But: considerably larger brain
 - 775 cc
 - about 75% bigger than 450 cc of *A. garhi*
 - slightly more human-like dentition
 - somewhat small molars for an australopithecine

- thinner enamel on molars than most australopithecines
- more parabolic dental arcade
- somewhat reduced chewing muscles
- could brainy *A. rudolfensis* be our ancestor?
- *Australopithecus habilis* (1.9-1.6 mya)
 - not too different from other australopithecines
 - short, fast juvenile development, like other australopithecines
 - slightly larger brain than most australopithecines, but not much
 - 500 cc
 - about 10% bigger than 450 cc of *A. garhi*
 - But: considerably more human-like teeth and cranium shape
 - more human-like dentition:
 - significantly smaller teeth in general
 - thinner enamel on molars than other australopithecines
 - more parabolic dental arcade
 - considerably reduced chewing muscles
 - more human-like cranium shape and features, other than brain size
 - smaller, lighter face
 - less prognathic
 - rounder braincase
 - less chunky base of cranium
 - could human-looking *A. habilis* be our ancestor?
- Plio-pleistocene paranthropines (species of *Paranthropus*) (2.5 to 1.0 mya)
 - in general
 - very like australopithecines from the neck down
 - small, bipedal bodies
 - adapted for extremely heaving chewing on the back teeth, even more so than australopithecines
 - huge molars
 - very reduced canines
 - zygomatic arches leave space for huge temporal muscles
 - zygomatic arches very heavy for attaching strong masseter muscles
 - massive mandible
 - tooth wear suggests eating hard seeds or nuts
 - probably two or more lineages of extreme chewers
 - one with very prognathic faces
 - one with fairly vertical faces
 - all extinct by 1.0 mya
 - clearly not our ancestors
- *Paranthropus aethiopicus* (2.5 mya)
 - the earliest of the known *Paranthropus* species
 - yet the most extreme chewer of all of them
- *Paranthropus robustus* (1.8-1.0 mya: relatively late)

- wear on animal bones found with *P. robustus* suggests that they used large splinters of animal bone to dig into anthills
- *Paranthropus boisei* (2.2-1.3 mya)
 - fairly vertical face, like *P. robustus*
 - versus very prognathic face of *P. aethiopicus*
- Possible descendent(s) of *Kenyanthropus*
 - no fossil evidence of them
 - descendants of *Kenyanthropus* would have resembled australopithecines
 - but without the heavy chewing adaptation
 - that is, with smaller molars, smaller temporal muscles, etc.
 - and with *Kenyanthropus*'s more vertical, human-like face
 - this would make *Kenyanthropus* a logical ancestor for humans
 - leaving australopithecines as a side branch that specialized on seeds, then went extinct
 - these descendants of *Kenyanthropus* could be the makers of the stone tool cutmarks found with *A. garhi* around 2.5 mya, rather than the small-brained *A. garhi*
 - only more fossils will resolve this
- The phylogeny is uncertain
 - many different phylogenies are possible, none clearly the best
 - were our ancestors...
 - australopithecines?
 - *Kenyanthropus*?
 - maybe *Kenyanthropus* via *A. rudolfensis*, but not the earlier australopithecines?
 - was *Sahelanthropus* in our lineage, or did it lead to gorillas, or did it go extinct?
- Whatever the phylogenetic relationships, we can be pretty sure that our lineage evolved from a Plio-pleistocene hominin generally similar to these, that:
 - was bipedal
 - thus terrestrial
 - but continued to spend a fair amount of time in the trees
 - had grinding molars and reduced canines
 - good for a wide range of foods
 - had considerable sexual dimorphism in body size
 - so it probably lived in multi-female, multi-male groups
 - with lots of male-male competition
 - had a brain comparable to a chimp's
 - except the late *A. rudolfensis*, considerably larger
 - had short, rapid juvenile development, like a chimp's
 - probably made
 - expedient tools of plant material, bone, etc.
 - simple stone tools (more on this later)
 - maybe hunted and ate some meat
 - based mostly on analogies to chimps