So far, we have seen how evolution works in general, and how it has shaped our closest relatives, the non-human primates.

Now we will shift gears again, and look at the direct evidence of how our own kind evolved.

We want to know basically two things:

- the sequence of steps that led from some kind of animal in the past to modern humans.
- the evolutionary reasons for each one of those steps.
  - why would our quadrupedal ancestors evolve into bipeds?
  - why would they develop language? … etc.

This is still an active field, with many questions left to be resolved.

This direct evidence comes from paleontology.

- the study of fossilized animal and plant remains
  - for animals, usually bones
  - occasionally, other body parts and evidence of them
- usually, when an animal or plant dies, the bones and other parts rot, weather, and decay away
  - under some rare circumstances, bones can be preserved as fossils
- the most common form of fossil is formed when the organic material gradually dissolves away and is replaced by minerals that crystallize out of ground water
  - this creates a rock in the exact shape of the bone
  - which is then very durable, and may last long enough to be found and studied
- the study of fossils is paleontology, done by paleontologists
  - most paleontologists study extinct animals (and plants) that are not primates, as the evolutionary arm of biology
- the study of fossils of animals ancestral to humans and our close relatives is a sub-specialty often called paleoanthropology, done by paleoanthropologists
  - by the way, archaeologists like me do not normally study fossils
    - we study the material evidence of cultural activity by people
      - that is, tools, houses, campsites, garbage dumps, burials, etc.
      - sometimes that includes the remains of human bodies or other animals
      - this stuff is usually much younger than any fossils

We can often determine the age of fossils.

- The book explains briefly how some of these methods work, but we won’t take the time to go through the physics of these methods here.

  - Potassium-argon dating tells us how long ago lava or ash cooled to a solid
    - but works only on rocks (not the fossils themselves)
    - and the rocks must have cooled from liquid at least half a million years ago
    - used by dating a layer of basalt (lava) from above the fossil and another from below it, to bracket the fossil’s age
  - Radiocarbon dating tells us how long ago a living thing died
    - but works only on organic material that is less than 70,000 to 50,000 years old
– most of human evolution occurred too long ago for the radiocarbon method to help
– and other methods…
– The point: we can tell how old fossils are, but with differing degrees of accuracy and precision, depending on the fossil’s age and the conditions where it was buried

– Many of these extinct animals evolved in a world very different from the one we know
– the continents were arranged differently
  – again, the book describes this briefly, but we won’t pursue it here
  – the story of how “continental drift” was discovered, proven, and the ancient world reconstructed is fascinating - take a geology course!
– the changing position of the continents and the oceans between them was important to primate evolution in two ways
  – it played a big role in forming the very different climates of the past, from tropical forest conditions that covered most of the globe, to the ice ages
  – it isolated some populations of primates from each other, like the New World monkeys from all the rest in Africa and Asia
– but most of the primate evolution that will interest us happened after the continents had split up into roughly their modern arrangement
  – so for this class, continental drift is not a crucial part of the story
– the climate differed drastically from today, and changed drastically during the evolution of the primates
  – we will have to take the climate and environment into account if we want to understand what was driving our ancestors’ evolution
  – the dinosaurs disappeared around 65 mya (million years ago)
    – at the end of the Cretaceous period and the beginning of the Tertiary period
  – the first primates appeared around 55 mya
    – near the peak of recent global temperatures, about 25° C (77° F)
    – compare to the global average temperature now, about 5° C (41° F), cold but not freezing
    – Effectively the whole earth was tropical, hot, wet, and densely forested
  – Since then, the temperature has generally been dropping, very irregularly
    – eventually going into a series of ice ages (glacial periods) separated by warm interstadial periods
    – it was in this period of extreme climate swings and relative cold that our own genus Homo first appeared
    – We happen to live in one of the warm periods between glacial periods, or interstadials, which started roughly 12,000 years ago
    – there is no particular reason to think it is any different from the past few interstadials, which generally lasted 30,000 to 50,000 years
– you might note: the difference between the cold parts of the ice ages and the warm interstadials (like the present) was only around 5° C (9° F)
– think about that next time you hear global warming experts talk about a likely change of many degrees C in the coming century… that would be climate change on the same scale as the swings between ice ages and interstadials, but in the opposite direction…
- Let’s begin the story of the origin of humans
- Picking up the story in the early Cretaceous period, around 350 mya (million years ago)
- The Earth was covered by gymnosperm forests
  - gymnosperms are plants that
    - bear seeds, generally in cones
    - have no flowers
    - and no fruit
    - depend on the wind to blow their pollen around to fertilize another plant to produce seeds
    - most have needle-like leaves
    - generally have a single stem with minor branches, like a Christmas tree
  - modern examples are pines and redwoods
  - visualize the world covered by coniferous forests
    - straight trunks, twiggy branches, needles
    - difficult to move from one tree to the next, few arboreal animals
  - this was the environment in which the dinosaurs first evolved, diversified, and became the most prevalent kind of animal
  - mammals also first appeared in this kind of environment, but they remained relatively few compared to the reptiles
- About 100 mya, during the Cretaceous period, a new type of plant emerged: the angiosperms
  - this was the later part of the time that reptiles dominated the land
  - angiosperms are plants that
    - have flowers
    - many of which depend on insects or animals to pick up pollen and redeposit it in order to fertilize the same flower or a different one to produce seeds
    - produce seeds enclosed in fruits, rather than cones, many of which are edible
    - have broad, rather than needle-like, leaves
    - have complex branches, like most familiar trees
  - most familiar modern plants are angiosperms, except conifers and ferns
  - imagine the world largely covered by tropical and temperate broad-leaf forests
    - like the ones in the pictures we have been seeing of primates
- angiosperms offered new possibilities for animals
  - the angiosperms co-evolved with animals
  - evolved showy flowers with edible nectar and fruits to attract animals to pollinate them
  - evolved edible fruits to get animals to disperse their seeds
  - many animals evolved specialized features to find, eat, and digest the angiosperm fruits and leaves
  - for the first time, many animals also developed arboreal habits
    - because angiosperm forests form interlocking canopies that allow movement from one tree to the next without dropping to the ground
- various mammals adapted to these new niches, including the precursors to the primates
  - adapted to eat insects and possibly seeds
– small bodies
– teeth with pointy cusps
– similar to modern tree shrews
– imagine tropical deciduous forests, with dinosaurs prevalent on the ground, and little
  shrewlike mammals scurrying around in the trees and underbrush

– Something drastic happened at the end of the Cretaceous period, around 65 mya
  – this is the famous “Cretaceous-Tertiary boundary”, or “K-T boundary”
  – many species of animals and plants abruptly went extinct
  – almost all of the dinosaurs disappeared
  – most geologists and paleontologists now believe that this was due to a massive meteorite
    striking the Earth
    – about 6 kilometers (3.5 miles) in diameter
    – the dust and vapor thrown up by the impact darkened the globe for several years
    – killing plants and plankton, temporarily cooling the climate, etc.
    – disrupting the food chain and driving many species extinct
  – but some of the small, nocturnal, rodent-like early mammals survived
    – these were our ancestors…

– About the same time that the dinosaurs went extinct, the first **plesiadapiforms** appeared
  – a late example: *Carpolestes simpsoni*
    – small, rodent-like variant of earlier mammals
    – but with opposable thumbs/toes with flat nails
      – retaining claws on the other digits
    – flattish molars suggest frugivorous diet
    – eyes are still on the side of the head, no overlapping stereo vision
    – no postorbital bar
    – hindlimbs still only slightly more powerful than forelimbs (locomotion not so hindlimb
      dominated as in primates)
  – so these animals had a few, but not all, of the suite of traits that define primates

– by about 10 million years later, some of these little mammals had evolved into the first definite
  primates
  – this was the Eocene epoch, about 55 to 36 mya
    – approaching the peak of recent global temperatures, about 25° C (77° F)
    – Effectively the whole earth was tropical, hot, and wet
    – most of the world was covered with tropical forest
  – there were two varieties of **Eocene primates**, both similar to modern strepsirrhines
    – **Adapids**, like modern lemurs
      – larger
      – smaller orbits (and therefore, eyes)
      – thus probably diurnal
      – frugivores and folivores
    – **Oomomyids**, like modern tarsiers
      – smaller
- larger eyes
  - thus probably nocturnal
- sharp teeth, probably for eating insects
- frugivores, insectivores and gummivores
- the full suite of basic primate features evolved in this environment
  - grasping hands and feet with opposable thumb/big toe
- nails, not claws, with grasping pads on fingers
- hindlimb-dominated locomotion
- reduced snout and sense of smell
- larger, forward-facing eyes with overlapping field of view
  - this is associated with a bar of bone behind the eye socket to support and protect the eyeball on the outside (post-orbital bar)
- larger brain relative to body size

- What was it about this environment that caused selection to favor the features of primates?
  - Arboreal hypothesis suggests that
    - primate features were advantageous for living in trees
    - grasping hands for holding onto branches
    - binocular vision for depth perception
    - reduced smell because smell was not as important for moving around in trees
    - brain became complex to deal with balance and complex navigation in branches
    - problem with the theory
      - lots of modern, successful arboreal animals do not have these characteristics
      - so there must be something else that favored the primate characteristics
  - Matt Cartmill’s visual predation hypothesis suggests that
    - primate characteristics were favored because they helped in catching insect prey
    - pro
      - stereoscopic vision is found in modern animals that use vision to locate prey, like cats
    - con
      - many living strepsirrhines use sound and smell to locate prey
        - so it seems unlikely that the common primate ancestor was a visual predator, because many strepsirrhine lineages would have to have lost those traits and reverted to a more ancient, generalized condition
    - plesiadapiforms (particularly Carpolestes simpsoni) evolved grasping hands and feet with neither stereo vision nor an insectivorous diet
      - so grasping hands/feet must have initially evolved for some other purpose
  - Leaping hypothesis suggests that
    - primate characteristics were favored because they helped in leaping locomotion
    - con
      - plesiadapiforms (particularly Carpolestes simpsoni) evolved grasping hands and feet without developing powerful leaping hindlimbs
      - so selection favoring leaping could not have led to the basic primate traits of grasping hands and feet
  - Diet shift hypothesis suggests that
early primates focused on insects
then, with increasing radiation of angiosperms, acute stereo vision, larger brains, and grasping hands were favored in order to exploit more varied food sources
- including fruit, flowers, gum
- good stereo night vision would have been important if they had to handle varied, small, complex items at night
- con
- plenty of animals have a varied diet and are nocturnal without selection having favored primate-like characteristics
- plesiadapiforms (particularly *Carpolestes simpsoni*) ate fruit without selection favoring stereo vision

**Two-step hypothesis**
- the basic primate traits did not evolve all together as a package, but instead evolved separately in two stages, for different reasons
- first, some mammals evolved to eat fruit, flowers, and nectar located at the ends of angiosperm branches (a “terminal branch” diet)
  - grasping hands and feet with flat nails helped to reach and collect this food
- later, these animals expanded their terminal branch diet by hunting insects found around the fruit and flowers
  - stereo vision helped in hunting the insects
  - snout was reduced as improved vision increasingly replaced smell for locating food
- this hypothesis fits with the fossils (for now!)
  - first, plesiadapiforms evolved grasping hands and feet
  - then, early primates added stereo vision

So far, we have seen only strepsirrhine-like early primates
the first haplorrhine (monkey-like) primates appeared in the Eocene
- but are still very poorly known

Much better evidence of haplorrhines by the beginning of the Oligocene
- 36 mya
  - lower temperatures, but still very warm by modern standards
  - more seasonal: wider temperature swings from winter to summer
- Fossils of **Oligocene primates** are found in the Fayum depression (Egypt)
  - at that time, a swamp
  - adapids (lemur-like) and omomyids (tarsier-like) continued, as before
  - plus ten new genera of haplorrhines
  - unknown whether haplorrhines evolved from omomyids or adapids, or some other as yet unknown Eocene primates
  - later in the Oligocene (33 mya), a famous species: *Aegyptopithecus zeuxis*
    - post-orbital bar, as in of all primates
    - plus post-orbital plate, as in haplorrhines
    - moderate sized eyes: diurnal
    - prognathic: jaws (snout) stick forward
foramen magnum (opening for the spinal cord) at back of head (not underneath): implies a quadrupedal posture, spine generally horizontal

- larger brain, but still not very big
- postcranial bones suggest arboreal
- 13 pounds
- large, wide, protruding (“procumbent”) incisors plus large, sturdy canines: typical of frugivores
- significant sexual dimorphism: probably multi-female groups with lots of male-male competition

- Some of these Oligocene primates were probably ancestral to, or close relatives of ancestors of, modern Old World monkeys and apes
- A few fossil haplorrhines are also found in South America (Bolivia and Argentina)
- also around 34 mya, about the same as the first haplorrhines in the Old World
- how did they get to the New World?
  - this presents some interesting problems that are covered in the reading
  - we don’t have time to discuss them here

- The book also has an excellent discussion of how incomplete the fossil record is
  - again, we don’t have time to cover this in class
  - the outcome is that we probably have seen fossils of only about 3% of all the primate species that have ever lived
  - real phylogenies are probably much bushier than the few fossils suggest
    - that is, more complex, more branches than we know
  - but even if fossils are not direct ancestors of particular living primates or other fossils, they are probably close relatives
  - so they give us a rough idea of what the actual ancestors were probably like

- the first known hominoids (apes) appeared in the late Oligocene, 27 mya
- example early Oligocene ape: genus Proconsul (probably various species)
  - lived in tropical rainforest
  - fairly large, like a macaque
    - 33-110 pounds
  - hominoid traits
    - no tail
    - no “fleshy sitting pads” (ischial callosities)
    - larger body size
    - various subtle skeletal similarities to modern apes
    - slightly larger brain to body size ratio
    - short forelimbs and narrow chest indicate they were quadrupedal, walking on top of branches, as many monkeys do
      - rather than hanging by arms, as modern apes do
    - teeth indicate frugivorous diet
      - thin enamel on the molars: relatively soft foods
- another Oligocene hominoid: Morotopithecus bishopi
  - similar to Proconsul, but with hints of more apelike posture and locomotion
− evidence: scapula (shoulder blade) suggests that it climbed and hung from branches, maybe brachiated

− the middle Miocene (15-10 mya) saw a great radiation of hominoids (apes)
− that is, the hominoids split into many different lines, with different species adapting to many different niches
− why? We don’t really know, but:
− lots of climate changes in the Miocene
− from the middle Miocene on, it got cooler and drier
− tropical forests shrank, and there were greater areas of open woodland and savanna
− the climate also began to change back and forth between warmer and cooler more rapidly, on a scale of just tens of thousands of years
− maybe these rapid changes, rather than the climate itself, was the key
− maybe something about apes made them well suited to handle changing environments
− maybe the ability to get by on a range of different foods, rather than being strongly committed to just one category of foods
− also, Africa and Eurasia got close and joined, cutting off the Tethys sea around 15-10 mya
− leading to an exchange of animals and plants
− probably changing the ecology in many ways
− and allowing some species of early apes (genus Proconsul) to spread out of Africa to more varied environments
− so populations of apes in different environments, surrounded by new varieties of plants and animals, evolved into many different species of apes
− most of which went extinct by the end of the Miocene or slightly later
− the many, varied Miocene hominoids (Miocene apes)
− Kenyapithecus, Oreopithecus, Dryopithecus, Sivapithecus, Ramapithecus, etc.
− general trend seems towards more chewing -- eating harder or more fibrous foods
− presumably in response to the drying, more seasonal climate
− which would have encouraged woodier, tougher plants compared to the tropical rainforest
− Miocene hominoids (apes) had features for heavy chewing
− molars of some species had thick enamel, allowing for more wear and more pressure to be applied to break hard seeds
− molars had lower, rounded cusps, better for grinding, less designed for shearing leaves
− that is, less specialized, more generalized for a varied diet
− molars tend to be worn from lots of grinding
− U-shaped dental arcade
− typical of apes, different from hominids
− more space for larger temporal muscles (that pull the lower jaw up against the upper jaw)
− this is visible by looking at the space where the temporal muscle passes between the temporal bone of the brain case and the zygomatic arch
− this whole space is filled by the temporal muscle
− more massive mandible (lower jaw), to withstand the increased chewing forces
at least two of the Miocene hominoids (*Dryopithecus* and *Oreopithecus*) were arboreal, adapted to hanging by their arms like quadrumanual or brachiating apes

− they have the classic anatomical adjustments to brachiation or quadrumanuality
  − wide ribcage
  − shoulder blades at the back, not on the sides
  − long arms, short legs
  − long, curved fingers
  − this is the first definite appearance of these classically apelike features, which clearly led eventually to humans
    − although *Morotopithecus* may have had some or all of them

− unknown exactly how these hominoids relate to living primates
  − we may not have found the species that were ancestral to the various modern hominoids (humans, gorillas, chimps, orangs, gibbons, siamangs)
  − except *Sivapithecus*, which looks to be the ancestor, or a relative of the ancestor, of orangutans

− by the late Miocene and early Pliocene, many varieties of Miocene hominoids were going extinct
  − only a few lineages survived
  − leading to the modern apes, and to us
  − there used to be many more kinds of apes in the world; now just a few remain

− By the early Pliocene, between 5 and 4 mya, one of the surviving ape lineages was starting to show signs of resembling us
  − these were the first hominins -- the lineage that led specifically to us
  − we will look at them next time.