

Paleontology and the first primates

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- 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
 - and 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 prosimians
 - **Adapids**, like modern lemurs
 - larger
 - smaller orbits (and therefore, eyes)
 - thus probably diurnal
 - frugivores and folivores
 - **Omomyids**, 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 prosimians use sound and smell to locate prey
 - so it seems unlikely that the common primate ancestor was a visual predator, because many prosimian 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 focussed 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 prosimian-like early primates
- the first anthropoid (monkey-like) primates appeared in the Eocene
 - but are still very poorly known
- Much better evidence of anthropoids 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 anthropoids
 - unknown whether anthropoids 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 anthropoids
 - 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 anthropoids are also found in South America (Bolivia and Argentina)
 - also around 34 mya, about the same as the first anthropoids 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 quadrumanal or brachiating apes
 - they have the classic anatomical adjustments to brachiation or quadrumanality
 - 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.