Chapter 4  

EVOLUTION IN THE FOSSIL RECORD

The fossil record reveals the existence of many creatures that have left no living descendants; of great episodes of extinction and diversification; and of the movements of continents and organisms the explain their present distributions.

The fossil record provides evidence on two particularly important themes:

- Phenotypic transformations in particular lineages.
- Changes in biological diversity over time.

SOME FUNDAMENTALS OF GEOLOGY

ROCK FORMATION

EARTH STRUCTURE

Radius of 6,357 km (3,948 miles) at the poles and 6,378 km (3,960 miles) at the equator.

Asthenosphere:

- Inner core 800 miles radius, solid iron.
- Outer core 1,300 miles radius, molten iron.
- Mantle 1,800 miles radius, molten rock.

Lithosphere:

- Upper part of the mantle.
- Crust 5-35 miles thick, solid rock.


ROCK TYPES

**Igneous**: solidified magma; about 65% of the crust, e.g. granite, lava flows, basalt.

**Sedimentary**: hardened eroded material due to pressure or chemical means; about 8% of the crust, e.g. limestone, sandstone, shale.

**Metamorphic**: any rock that have undergone further change due to pressure, heat and chemical reactions; about 27% of the crust, e.g. marble from limestone.

[http://www2.nature.nps.gov/geology/USGSNPS/rxmin/rockchart.pdf](http://www2.nature.nps.gov/geology/USGSNPS/rxmin/rockchart.pdf)
PLATE TECTONICS

“The study of the structure of the earth's crust and mantle with reference to the theory that the earth's lithosphere is divided into large rigid blocks (plates) that are floating on semifluid rock and are thus able to interact with each other at their boundaries, and to the associated theories of continental drift and seafloor spreading.”

The drifting of tectonic plates on the Earth's surface relative to each other.

It is an on-going process that has changed the configuration of the continents since their formation in Archean time about.

This hypothesis first proposed in 1912 by Alfred L. Wegener, a German Meteorologist, was not widely accepted until after 1960.

Wegener's evidence for continental drift includes:

(1) Continental fit.

(2) Glacial deposits indicating high latitudes on portions of the continents that are now in warm latitudes,

(3) Alignment of geologic features such as mountain belts when continents are reassembled, and

(4) Occurrence of identical fossils, of the same age, on landmasses that are no longer connected.

Other evidence:

(5) Palaeomagnetism. Ferrous material in new igneous rocks becomes magnetized in a direction that depends on the magnetic field at the time.

- Old rocks in Africa and South America show different magnetic orientation while new rocks show similar orientation.

- The polar pathways of South America and Africa coincide when the two continents are fitted together.

(6) Sea floor spreading due to the molten material emerging at the oceanic ridges and spreading on each side of the ridge.

- The new rocks become magnetized according to the orientation of the magnetic field prevailing at the time

- With time magnetic fields change in strength and direction and material become magnetized differently forming similar belts of magnetized rocks on each side of the ridge.

http://www2.nature.nps.gov/geology/USGSNPS/pltec/platesSH.pdf
http://www2.nature.nps.gov/geology/USGSNPS/pltec/converg.pdf
GEOLOGIC TIME

Big Bang Theory: Origin of universe between 15-20 billion years ago.

Evidence:

- Hubble and the Red Shift
- The Expanding Universe
- Origin of Galaxies and the Solar System

Earth Chronology:

- 4.6 BY earth formed (BY = billion years)
- 4–3.8 BY life originated
- 3.7 – 3.8 BY oldest known fossils
- 2.5 BY photosynthesis, oxygen accumulated
- 1.5 BY first eukaryotes
- 800 MY soft-bodies multicellular life (MY = million years)
- 540 MY hard-bodied multicellular life

Arrhenius and Mojzsis have estimated that life on Earth was present before 3.85 billion years ago. They conducted studies in sedimentary rocks in Greenland.


Ages of geological events can often be determined by radiometric dating, which measures the decay of certain radioactive elements in minerals that form in igneous rock.

http://www2.nature.nps.gov/geology/USGSNPS/gtime/ageofearth.pdf

The decay of radioactive parent atoms into stable daughter atoms occurs at a constant rate.

Each radioactive isotope has a specific half-life, e.g. the half-life of U-235 is about 0.7 billion years.

Long before radioactivity was discovered, geologists had established the relative ages of sedimentary rock formations, based on the principle that younger sediments are deposited on top of older ones.

Layers of sediments deposited at different times are called strata (sing. stratum).

About methods used to date rocks: http://www.talkorigins.org/faqs/faq-age-of-earth.html
Other sites: http://pubs.usgs.gov/gip/geotime/age.html
http://www2.nature.nps.gov/geology/USGSNPS/gtime/ageofearth.html
http://www2.nature.nps.gov/geology/USGSNPS/gtime/gtime1.html

THE GEOLOGIC TIME SCALE
Most of the eras and periods of the geologic time scale were named and determined by geologists that did not know about evolution. This was done before Darwin’s time.

These eras and periods are recognized by their fossil components.

The time boundaries of the different sectors of the scale are approximations and they change as more information becomes available, and with the opinion of the geologists.

Eras are divided into Periods and those into Epochs. See table 4.1, p. 76.

The Phanerozoic time is divided into three Eras: Paleozoic, Mesozoic, and Cenozoic.

1. Paleozoic began about 542 My.
2. Mesozoic began about 245 My.
3. Cenozoic began about 65 My.

Interesting site:
http://www2.nature.nps.gov/geology/USGSNPS/gtime/gtime2.html
http://www.geo.ucalgary.ca/~macrae/timescale/timescale.html

FOSSIL RECORD

On the whole the fossil record is very incomplete.

The record is incomplete for several reasons:

1. Delicate organisms seldom become fossilized or live in environments where decay is rapid.
2. Sediments form at intervals and contain only part of the organisms that lived in the region.
3. For fossils to form, the organisms must first become solidified into rock, and rock must survive millions of years without being eroded, metamorphosed or subducted, and then become accessible to paleontologists.
4. Species that evolved elsewhere may appear in a locality after having migrated into the area.

About 250,000 fossil species have been described and represent an estimated 1% at the most of all species that have lived in the past.

EVOLUTIONARY CHANGES WITHIN THE SPECIES

Some records have preserved the changes of a single species. These changes tend to be gradual and independent of each other.

Changes in a single unbranching lineage are called anagenesis.

See the evolution of the shape of the shell of Contusotruncana on page 78, fig. 4.3.
ORIGINS OF HIGHER TAXA

Macroevolution is the term used to describe the origin of higher taxa over long periods of geologic time.

THE ORIGINS OF AMPHIBIA (TETRAPODS)

The class Sarcopterygii is extremely ancient in origin, their first remains appearing in Lower Devonian strata of Germany, about 408 million years old.

The most important group, the rhipidistians, which gave rise to the amphibians by the end of the Devonian, became extinct about 120 million years later, near the beginning of the Permian.

Two lesser groups, the coelacanths and the dipnoans (lungfishes), have barely survived. They had a tail fin and fleshy, paired fins, with a central axis of several large bones to which lateral bones and slender, jointed rays articulated.

Recognition of the class Sarcopterygii is controversial in that some ichthyologists believe that the two major groups, the Crossopterygii (including the rhipidistians and coelacanths) and the Dipnoi, have arisen from independent origins, the present structures of the two groups being widely divergent.

Osteolepiforms (crossopterigians) and dipnoans were the first fishes to develop lungs by the end of the Devonian (410-360 m.y.a.)

By the end of the Devonian (360 m.y.a.) the transition from rhipidistian-osteolepiform fish to tetrapod amphibian had occurred.

Similarities between early amphibians and osteolepiforms;

- Similar shape and position of dermal skull bones.
- Homologous fins and leg bones.
- Tooth structure: similar complex **labyrinthine pulp**.
- Sensory lateral line extends into the skull of osteolepiforms appear similar and homologous to skull canals of early tetrapods.
- Early amphibians had fin-rayed caudal tail.
- Similar vertebrae.

The earliest amphibians on record are Acanthostega and Ichthyostega. Both show relationship to rhipidistians.

- Acanthostega was an early tetrapod that was ill suited for life on land. It has internal gills and led an aquatic life.

- Ichthyostega lived in the Late Devonian and had scales and dorsal tail fin. Advanced traits shared with more advanced amphibians include typical early amphibian limbs and limb supports, the lack of gills, and strong ribs. The head could be flexed relative to the body by flexible neck. They had pectoral and pelvic girdles. It used lungs as the primary means to obtain oxygen.
In Ichthyostega, the forelimbs seem to have been weight-bearing, but the forearm was unable to extend fully. Only one articulated specimen shows a femur in association with a body and forequarters. The shoulders were massive compared with the much smaller and paddle-like hind limb, in contrast to the more conventional proportions that it is usually given.

The proportions of an elephant seal appear the closest analogue among living animals. Perhaps Ichthyostega hauled itself up shelving beaches, moving its forelimbs in parallel and dragging its hindquarters along (Clack 1997).

Other important fossils that show intermediate stages between fins and limbs plus other skeletal features are Panderichthys and Tiktaalik.


ORIGIN OF BIRDS

Birds may have evolved from small bipedal, ground-dwelling endothermic carnivorous reptiles. Their feathers probably derived from scales. Because of the many fossils found in recent years, the distinction between birds and dinosaurs has become arbitrary.

Theory of a Direct Thecodont Origin of Birds

- Birds evolved directly from thecodonts.
- Theropod dinosaurs are a side branch of reptilian evolution, parallel to that of birds.

Theory of a Theropod Origin of Birds

- The first proto-birds probably evolved in the Late Jurassic (160-145 m.y.a) from a group of theropod dinosaurs related to the Coelosaurians.
- Theropods had in turn evolved from theropods.

Theropod dinosaurs were carnivorous reptiles that share the following anatomical structures with birds: presence of a furcula, the wishbone; air spaces in the bones; three toes; some had feathers; and they incubate the eggs.

The only lineage of endothermic archosaurs to survive into the Cenozoic was the Neornithes or "modern birds".

The two most primitive birds accepted by most scientists are Archaeopteryx and Confuciusornis.

Additional reading of the controversy about the origin of birds: http://www.sciencemag.org/content/280/5362/355.full

ARCHAEOPTERYX

The first feathered fossil from the Upper Jurassic, 150 m.y.a.
- Found in 1860 in a limestone quarry from Bavaria.
- Very similar to reptiles.
- Feathers
- It could fly although weakly.
- Light bones and were fast and agile.
- Long slender necks, large back legs, and long counter balancing tails.
- Bipedal stance.

Birds show some characters that were present in early dinosaurs and then were lost, e.g. wishbone.

"Dinosaurs had a strong wishbone in their primitive state, but had lost it through evolution. In the early 1900's, anatomists, most notably Gerhard Heilman in 1926, refused to believe that an animal could recall a lost part of it’s anatomy. They said that birds could not have been descended from dinosaurs, because dinosaurs had already lost their wishbone, and that any similarities between coelurosaurs and birds were the result of evolutionary convergence. Recent finds have shown that a number of the coelurosaurs had re-evolved collarbones (Norman 1994). Studies have shown that a suppresser gene prevents a primitive gene from expressing itself. When that gene does not work, the older trait expresses itself. There are many examples where a suppresser gene does not work, and it can be seen even today. From time to time, a healthy human baby is born with a tail protruding from it. Whales have been hauled in with fully developed legs sticking out of the side of its body, a throwback to a time when they were land borne predators. The most unusual example is of a bird from South America known as a Hoatzin. As a chick, it shows a wing structure remarkably similar to Archaeopteryx. It has claws on its wings that it uses to climb up and down in the foliage to escape predators. If its wing is placed next to an Archaeopteryx specimen, the similarities are striking. This bird has recalled a primitive trait from genetic storage and Natural Selection has acted upon it to the point where it has re-established itself. This trait enables the chick to have a better chance of surviving to adulthood, where the wing bones fuse and look like any other birds (Bakker 1986)."

http://www.micro.utexas.edu/courses/mcmurry/spring98/21/justin.html

See the following website where a list of similarities between birds and dinosaurs is published:
http://9e.devybio.com/article.php?ch=16&id=161
http://evolution.berkeley.edu/evolibrary/article/evograms_06

Archaeopteryx and the 30 million year younger Confuciusornis have several traits in common.

- They both have three claws on their wings.
- The fingers are not fused.
- The wishbone is almost identical and the breastbone is small.

There are also some traits that separate them:

- The tail is longer in Archaeopteryx, while the claws are stronger in Confuciusornis.
- Archaeopteryx has teeth while Confuciusornis has a beak.

Confuciusornis was found in Liaoning Province, China and is about 120-140 million years old.
Confuciusornis is the earliest known bird that could fly well. Its wings were rather crude, but it was equipped with features seen in today's birds, such as lightweight bones and a shorter, rudder-like tail. It had a toothless beak.

Caudipteryx zoui is another intermediate species from China, from the Middle Cretaceous, 120 m.y.a. It was a fast runner with feathers but incapable of flight.

Ichthyornis and Hesperornis were Late Cretaceous birds that had teeth like Archaeopteryx but show several more advanced features. These two species resemble modern seabirds in their anatomy. Both of these species had...

- Deep set teeth that curved backwards indicating a fish diet.
- Ichthyornis had a wide crest to support its flight muscles, but it more closely resembled that of a dinosaur than a bird.
- It also had flat dinosaur style joints in its vertebrae.
- Both of these birds had lost the long tailed trait of the dinosaurs in favor of the modern "parson’s nose” style of today’s birds.
- These birds supported a pattern from dinosaur, to primitive bird, to more modern ones, to fully modern ones.
- Next feathered fossils come from the Cretaceous about 110 million years later and they are mostly shorebirds.

Feathers:
- No record of when and how they evolved, e.g. scales?
- Were they primarily for insulation or for flying?
- Did they develop in arboreal reptiles for gliding or in ground dwelling animals for running faster (cursorial)?

An opinion about the origin of feathers:

"The proteins that make feathers in living birds are completely unlike the proteins that make reptilian scales today. Feathers originate in a skin layer deep under the outer layer that forms scales. It is very unlikely that feathers evolved from reptilian scales, even though that thought is deeply embedded in the minds of too many paleontologists. Feathers probably arose as new structures under and between reptile scales, not as modified scales. Many birds have scales on their lower legs and feet where feathers are not developed, and penguins have such short feathers on parts of their wings that the skin there is scaly for all practical purposes. So there is no real anatomical problem in imagining the evolution of feathers on a scaly reptilian skin. But feathers evolved in theropods as completely new structures, and any reasonable explanation of their origin has to take this into account.”

http://mygeologypage.ucdavis.edu/cowen/historyoflife/feathersandflight.html

Archaeopteryx had feathers very similar to the primary flying feathers of modern birds.

Sinosauropteryx had body feathers but their function is unknown; their function could have been for insulation.

Bird evolution moved fast from the Cretaceous through the beginning of the Tertiary and modern features appeared…

- Fused bones, enlarge keeled sternum, increase brain size, loss of teeth, loss of claws in the hands.
There is no clear reason why modern birds do not have teeth. One hypothesis is that the reduction and modification of forelimbs for flight, did not allow the birds to manipulate food into the proper position in the mouth, e.g. head first, for swallowing. Then, the teeth disappeared and the beak, a large scale on top of the mouth evolved.

By the Oligocene (55 m.y.a.) most modern bird orders had appeared.

The distinctive synapomorphy of the Aviales is the **opposable hind toe**, and no longer the feathers.

**ORIGIN OF MAMMALS**

Mammalian characteristics evolved mostly during the Mesozoic era (245-65 m.y.a.).

Mesozoic era consists of the Triassic (245-208 m.y.a.), Jurassic (208-146 m.y.a.) and Cretaceous (140-65 m.y.a.) periods.

Mammals have unique skeletal structures. We refer to them as diagnostic characters. **Characteristics**

Soft-body parts:

1. Mammary glands.
2. Live birth except for monotremes.
3. Hair covering and sweat glands to control temperature (endotherms).
4. Diaphragm to increase inspiration of oxygen.
5. Four-chambered heart.

Skeletal features:

1. Double occipital condyle for articulation with the first vertebra.
2. Mandible consisting of a single bone rather than several bones as in reptiles.
3. Jaw articulation between the squamosal and dentary bones rather than between the articular and quadrate bones as in other tetrapods.
5. Ear ossicles derived from the reptilian quadrate and articular bones.
7. Large braincase.
8. Heterodont dentition: greater differentiation among teeth, e.g. incisors, canines, multicusped premolars and molars.

Soon after the first amniotes originated in the Carboniferous, they gave rise to the Synapsida, a group characterized by an opening called temporal fenestra behind the eye socket, which probably provided space for enlarged jaw muscles to expand into it when contracted.

Synapsid reptiles first appeared in the Carboniferous (~365-290 m.y.a.).

- Strong evidence indicates that pelycosaurs (synapsids) are close to the line that gave rise to the therapsids.
Pelycosaurs appeared before the dinosaurs.

The primitive mammal-like reptiles, the Pelycosauria, became extinct during the Permian.

They left behind a variety of advanced mammal-like reptiles collectively termed the Therapsida.

By the Permian (290-245 m.y.a.) they had evolved into therapsids (synapsids) primarily adapted to a terrestrial existence.

Therapsids are often called "mammalian-like reptiles".

Permian synapsids, in the Order Therapsida, had large canine teeth, and the center of the palate was recessed, suggesting that the breathing passage was partially separated from the mouth cavity; their hind legs were rather vertical more like mammals than reptiles.

The therapsids show a chain of evolutionary steps towards mammals:

- Differentiated teeth and skull development.
- Jaw articulation, consolidation of the jaw bones,
- Development of mammal ear bones, palate, pelvis consolidation, scapula with spine, and leg positioning.

By the early Triassic (245-208 m.y.a.) some therapsids had become endotherms.

Cynodonts were an advanced group of therapsids that arose in the very late Permian and show several steps in the approach toward mammals.

The skeleton of cynodont therapsids was mammal-like and distinct from that of other reptiles.

- Vertical stance, knees pointing forward, elbows pointing backward.
- The rear of the skull was compressed giving them a dog-like appearance.
- The jaw articulation was still reptilian.
- Later therapsids had a mandible entirely composed of dentary bone.
- It’s here that we first see a secondary palate,
- The dentary became elongated, and the dentary and the squamosal became articulated more similar to that of mammals.
- Cheek teeth had multiple cusps,
- Two occipital condyles,
- Vast expansion of the temporal fenestra, with a great deal of transmission of jaw musculature

Development of specialized teeth: heterodont dentition.

Teeth developed cusps for chewing.

Mammals have to breathe continuously even when eating; this necessity developed the bony palate, and separates air entering the pharynx from food being chewed in the mouth.

In amphibians and terrestrial reptiles, the nasal openings are in the anterior portion of the mouth, and the animal has to temporarily interrupt breathing while the mouth is full of food.
Two of the great innovations of Cynodonts, which lead directly to mammals, are the development of occlusion and single replacement of teeth (i.e. two sets).

- **Occlusion** = the meeting of molars and premolars to grind over one another to process food more efficiently.
- **Single-replacement** = two sets of teeth, probably to ensure accurate occlusion and suckling.

Morganucodont was almost a mammal, with typical mammalian teeth and a lower jaw composed almost entirely of the dentary. The jaw had a double articulation with the skull.

- The articulation of the quadrate and articular bones together with the stapes closely approach the condition in modern mammals, in which these bones transmit sound to the inner ear.

The recently described Hadrocodium (Luo et al, 2001), from the Jurassic, is almost a mammal.

- The articular and quadrate bones are separated from the lower jaw and fully lodge in the middle ear;
- The lower jaw consists fully of the dentary.

The fossil record shows that mammalian characters evolved gradually.

The evolution of mammals from synapsids was gradual over a period of 130 million years and there is no cut-off point to recognize the mammals. The distinction is arbitrary.

**ORIGIN OF THE CETACEA**

Whales and dolphins form the Order Cetacea and evolved from terrestrial forms.

Their closest living relatives among the mammals are hippopotamuses; this is based on molecular evidence.

Some zoologists think that they should be included in the Order Artiodactyla together with the pigs, camels and ruminants (cows and antelopes).

Living cetaceans are highly modified mammals adapted to aquatic life.

**Characteristics of the Cetacea:**

1. Uniquely shaped tympanic bone that completely encloses the ear,
2. A nasal opening far back on top of the skull,
3. Stiff elbow, wrist and finger joints, all enclosed in a paddle-like flipper,
4. Rudimentary pelvis and hind limbs disconnected from the pelvis,
5. Lack of fused, differentiated sacral vertebrae that land mammals have.
6. Toothed whales have a large cavity in the lower jaw, the foramen that contains a sound transmitting pad of fat.

**General stages of the evolution of the cetaceans:**
- **Eocene raoodids**: hippo-like artiodactyl resembling the probable ancestor of the cetaceans. They were terrestrial but show some semiaquatic features.
- **Pakicetus** (53-48 My): probably semi-aquatic with a tympanic bone resembling that of modern cetaceans.
- **Ambulocetus** (48-47 My): adapted to living in shallow coastal waters; used its legs for swimming; digits end in small hooves like those of artiodactyls; mandibular foramen larger than in pakicetids; predator with long jaws.
- **Rodhocetus** (49-39 My): swam in its hind legs; fusion of sacral vertebrae was reduced; the pelvis was weak and could not support the animal on land; tooth form was simpler; nasal opening was farther back from the tip of the snout.
- **Dorudon** (35 My): was fully aquatic and used the tail for propulsion; the non-functional pelvis was disconnected from the vertebral column and the hind limb barely projected from the body; teeth are simpler; nostril is far back in the skull; front limbs are flipper-like with almost inflexible wrist and elbow.
- **Modern harbor porpoise**: blowhole is far back on the top of the head, accounting for the peculiar shape of the head; have no residual hind limbs.

**THE HOMININ FOSSIL RECORD**

DNA sequences imply that the closest relatives to humans are the chimpanzees.

The term “hominin” has been applied to the sister group of the chimpanzees.

The evolution of modern humans show through many intermediates from ape-like ancestors.

**There is disagreement** about how many species and genera of hominins should be recognized because

- Fossil specimens are too few, and too widely separated in time and space,
- Many differences are quantitative (differences in degrees) and often rather slight so it is difficult to determine which species is ancestral or collateral to the ancestral one.

The overall pattern of evolution is clear but the specific phylogenetic relationship between the taxa is not.

In the late Miocene about 8 m.y.a. the homininae (chimps, gorillas and humans) split from other apes.
- Supported by molecular data.

There is no agreement about the time when humans and chimps split (data varies between 7.7 and 3.5 m.y.a.).

- 3.5 - 5.5 m.y.a divergence proposed by Sarich and Cronin (1976).
- 5.5 - 7.7 m.y.a proposed by Sibley and Alquist (1984, in Chapter 12).
- 4.9 m.y.a proposed by Horai et al. (1995).
- 5 to 7 m.y.a. are the most common time given in present literature. This estimate is based mostly on DNA information.
Interesting reading: [http://www.evolutionpages.com/homo_pan_divergence.htm](http://www.evolutionpages.com/homo_pan_divergence.htm)

**Sahelanthropus tchadensis**, from the late Miocene, 6 – 7 My, is most primitive known hominin.

- Small canines,
- Flat face,
- Almost certainly bipedal

**Orrorin tugenensis** lived about 6 M.y.a.

**Ardipithecus kadabba** about 5.8- 5.2 My old.

**Ardipithecus ramidus** lived about 4.5 - 4.3 M.y.a in what is now Ethiopia.

**Australopithecus anamensis** is about 4.2 – 3.9 My old.

**Kenyanthropus platyops** is about 3.5 My old.

**Australopithecus afarensis** (3.5 My old) has been the most informative fossil and had the following primitive characteristics not far removed from the common ancestor of humans and chimpanzees …

- Prognathism
- Long arms and legs
- Large canines
- Small brain
- Curved bones in fingers and toes for climbing trees

And the following advanced characteristics…

- Pelvis and hind limbs are for walking upright; it was a bipedal animal.

In the Pliocene (5.3 M.y.a) and Pleistocene (1.8 M.y.a), the number of hominin species was probably very diverse.

A lineage of “robust” australopithecines named **Paranthropus**, had large molars and premolars and other features adapted to powerful chewing of tubers and hard plant material.

**Australopithecus africanus** (3.0 – 2.5 M.y.a) had large molars and premolars adapted for powerful chewing; they probably fed on tubers and coarse plant material. A. africanus had greater brain capacity than A. afarensis.

The increased cranial capacity is noted by the change in genus designation from Australopithecus to Homo.

**Homo habilis** was small, slightly more than chimp sized, but with cranial capacities of 600-800 cc, increased blood vessels in the head and brain, and increased flexibility of fingers and wrists. Some authors think that it can be assigned to Australopithecus.

- The earliest fossils assigned to the genus Homo are 1.9 – 1.5 M.y.a, late Pliocene and early Pleistocene.
- They are variable enough to be assigned to three species by some paleontologists: H. habilis, H. ergaster and H. rudolfensis.
The oldest specimens are similar to A. africanus and the younger one intergraded gradually with Homo erectus.

Limbs retain the ape-like proportions but the structure of the leg and foot that its bipedal locomotion was like that of humans.

H. habilis is associated with stone tools and cut animal bones: Olduwan technology.

**Homo erectus** lived from about 1.8 M.y.a to 200,000 years ago.

Homo erectus has been split into three species: Homo ergaster, H. heidelbergensis and H. erectus.

Some paleoanthropologists consider H. ergaster to have evolved into Homo sapiens.

Most authorities think that habilis, ergaster and sapiens are a single evolutionary lineage.

- Face became more vertical with a less projected jaw.
- The skull is rounded.
- Teeth are smaller
- Cranial capacity is between 800 to 1100 cm³.
- By about 1.8 m.y.a erectus had migrated out of Africa into Asia and specifically to Java. Approximately 1 m.y.a the tool kits begin to include tear-drop shaped hand axes and cleavers of uniform proportions. These tools are found throughout Africa and Europe, but not in Asia.

[http://anthro.palomar.edu/homo/homo_2.htm](http://anthro.palomar.edu/homo/homo_2.htm)

Homo erectus fossils persist until about 0.5 m.y.a. At that point, 500 – 300 Kya, grades into forms more sapiens-like, including skeletal changes and increasing cranial capacity to its modern 1400 cc. This prompts a change in species name to Archaic Homo sapiens.

These fossils are often subdivided into several subspecies such as rhodesiensis in Africa and neanderthalensis in Europe and the Middle East.

**Some authorities consider the Neanderthals** as a separate species of Homo: Homo neanderthalensis.

- Neanderthals had cranial capacities of about 1600 cc (modern humans average 1400 cc) but with skulls that sloped back from the brow ridges and with a pronounced bulge at the back of the skull.
- They were big game hunters who survived from about 300,000 BC to 35,000 BC.
- Their skeletons show an increasing divergence from the gracile body plan of the other Homo species as they were adapted to the frequent glacial stages of Europe during this time.
- Neanderthals coexisted with modern Homo sapiens in the Middle East from about 80,000 BC to about 40,000 BC, and in Europe from about 45,000 BC to 35,000 BC.
- We find the first evidence of intentional burials, sometimes with grave goods, among neandertalensis.
We also find evidence of individuals who were crippled during their lifetimes, yet were cared for and lived on for years with significant handicaps.

**Modern Homo sapiens** skeletons appear in Africa between 200,000 and 100,000 BP.

- In the Middle East excavations at Skhul cave have also provided evidence of early Homo sapiens.
- The tool kits they used began to include blades (with length twice the width) struck off of cores.
- We find the earliest preservation of evidence of artistic expression among modern H. sapiens in the form of beads, carvings, and cave paintings.
- Tool kits also begin to vary more rapidly from region to region and through shorter periods of time.

The Upper Paleolithic culture emerged about 40,000 years ago and several cultural styles appeared successively in Europe, e.g. Aurignacian and Mousterian.

Self-adornment, art, mythical and religious beliefs become more evident after 35,000 years ago.

A recent discovery in the island of Flores, Indonesia, of dwarf hominin material, dated about 18,000, is controversial. Scientists are not sure whether this represents a genetically different population or a pathological condition in the standard Homo sapiens.

Agriculture appeared about 11,000 to 10,000 years ago.

It is unknown at present if these cultural advances were associated with genetic changes.

**PHYLOGENY AND THE FOSSIL RECORD**

There is a very imperfect correlation between the relative times of origin of some taxa, as inferred from phylogenetic analysis, and their relative times of appearance in the fossil record. In other cases, the agreement is strong.

This correspondence is imperfect.

- Imperfect fossil record
- A group that originated in the distant past might be recovered only from recent deposits.
- An ancient lineage may have acquired the diagnostic characters much later.

The sequence in which the fossils appear matches phylogeny.

**EVOLUTIONARY TRENDS**

The fossil record shows many evolutionary trends.

In many cases those trends show a reversal to an earlier form.

Some features may have never reverted because they were advantageous or even necessary. E.g.:
• Feathers of penguins remain because they are insulating and are used in sexual displays in penguins and ostriches respectively.
• The notochord has not disappeared because it induces the development of the central nervous system.

Some cases may be truly irreversible because the developmental foundation of some characters has been lost in evolution.

Dollo’s Law: complex characters once lost, are not regained. Evolution is irreversible.

Dollo himself explicated his law as follows (1913): “The irreversibility of evolution is not simply an empirical law resting on facts of observation, as many have believed. It has deeper causes which lead it, in the last analysis, to a question of probabilities as with other natural laws....In order for it [evolution] to be reversible, we would have to admit the intervention of causes exactly inverse to those which gave rise to the individual variations which were the source of the first transformation and also to their fixation in an exactly inverse order – a circumstance so complex that we cannot imagine that it has ever occurred.”

Many lineages often pass through similar stages called grades. This generalization is called Cope’s Rule.

• Tendency of lineages to increase in size.
• Cope’s Rule has been abandoned by many scientists.


PUNCTUATED EQUILIBRIA

Gradual transition from one form to another is not always found in the fossil record.

Intermediate stages in the evolution of higher taxa are often unknown.

These gaps are usually explained by the incompleteness of the fossil record.

Eldredge and Gould proposed in 1972 a new explanation:

• Punctuated equilibrium: short periods of rapid change and macroevolutionary events during which new taxa arise (speciation) interrupt long periods of little change called stasis.
• The abrupt appearance of closely related species, not the appearance of higher taxa.

This hypothesis contrasts with the one called “phyletic gradualism”, the traditional hypothesis that proposes a gradual change over a long period of time.

The fossil record offers examples of both punctuated equilibrium and phyletic gradualism.

The hypothesis proposed by Eldredge and Gould is based on the model known as “founder effect speciation” or “peripatric speciation” proposed by Ernst Mayr in 1954.
• A new species appears suddenly in the fossil record because they evolved in small populations separated from the ancestral species and then, fully formed, migrated in the region where the fossil samples were taken. The evolutionary change may have been gradual but rapid and off-stage.

Eldredge and Gould also proposed that changes in morphology occur in association with the evolution of new species, speciation. This hypothesis is not widely accepted because it seems to contradict fossil record evidence.

• The fossil record shows that characters may evolve in between long-stable states in populations that do not undergo speciation.

• This pattern has been called punctuated gradualism.

Random fluctuation in a character may result in a gradual net change over time.

Consistent directional change was seldom recorded, perhaps because it often occurs too quickly to be preserved in a coarse fossil record.

http://www.talkorigins.org/faqs/punc-eq.html
http://en.wikipedia.org/wiki/Punctuated_equilibrium
http://www.sersc.org/journals/IJBSBT/vol3_no4/3.pdf

RATES OF EVOLUTION

The rate of evolutionary change varies greatly between characters, among evolving lineages and with the same lineage over time.

Individual features typically display a low rate of evolution, averaged over long periods of time, but more detailed fossil records show rapid, short-term fluctuations in characters.

Scientists often use the unit called the haldane to measure the mean change of a character per generation.

• The haldane is a measure of the evolutionary change using the number of standard deviation by which a character mean changes per generation.
• Standard deviation is a measure of the amount of variation within a population.

When rates of character evolution have been measured for ancestor-descendant series of dated fossils, the most striking result has been that average rates of evolution are usually extremely low.

• Measurements show an average rate of change over a long period of time.

Long-term averages conceal rapid evolutionary rates if the rate fluctuates or if the character fluctuates rapidly but show little net change.

• Fluctuation refers to long periods of no change alternate with bursts of rapid change.

We would expect higher rates if the measurements are made over shorter intervals of time.
Evolutionary rates can be very rapid, but they are not sustained at high rates for very long.

Other resources: