Chapter 34 - Vertebrate Evolution and Diversity

Introduction

- Humans and their closest relatives are vertebrates.
  - This group includes other mammals, birds, lizards, snakes, turtles, amphibians, and the various classes of fishes.
  - They share several unique features including a backbone, and a series of vertebrae.

Invertebrate Chordates and the Origin of Vertebrates

- The vertebrates belong to one of the two major phyla in the Deuterostomia, the chordates.
- The phylum Chordata includes three subphyla, the vertebrates and two phyla of invertebrates, the urochordates and the cephalochordates.
- Four anatomical features characterize the phylum Chordata
  - Although chordates vary widely in appearance, all share the presence of four anatomical structures at some point in their lifetime.
    - These chordate characteristics are a notochord; a dorsal, hollow nerve cord; pharyngeal slits; and a muscular, postanal tail.
      - The notochord, present in all chordate embryos, is a longitudinal, flexible rod located between the digestive tube and the nerve cord.
        - It is composed of large, fluid-filled cells encased in fairly stiff, fibrous tissue.
        - It provides skeletal support throughout most of the length of the animal.
        - While the notochord persists in the adult stage of some invertebrate chordates and primitive vertebrates, it remains as only a remnant in vertebrates with a more complex, jointed skeleton.
        - For example, it is the gelatinous material of the disks between vertebrae in humans.
      - The dorsal, hollow nerve cord develops in the vertebrate embryo from a plate of ectoderm that rolls into a tube dorsal to the notochord.
        - Other animal phyla have solid nerve cords, usually located ventrally.
        - The nerve cord of the chordate embryo develops into the central nervous system: the brain and spinal cord.
      - Pharyngeal gill slits connect the pharynx, just posterior to the mouth, to the outside of the animal.
        - These slits allow water that enters the mouth to exit without continuing through the entire digestive tract.
        - In many invertebrate chordates, the pharyngeal gill slits function as suspension-feeding devices.
        - The slits and the structures that support them have become modified for gas exchange (in aquatic vertebrates), jaw support, hearing, and other functions during vertebrate evolution.
      - Most chordates have a muscular tail extending posterior to the anus.
        - In contrast, nonchordates have a digestive tract that extends nearly the whole length of the body.
        - The chordate tail contains skeletal elements and muscles.
        - It provides much of the propulsive force in many aquatic species.
- Invertebrate chordates provide clues to the origin of vertebrates
  - Most urochordates, commonly called tunicates, are sessile marine animals that adhere to

rocks, docks, and boats.
- Others are planktonic.
- Some species are colonial, others solitary.
- Tunicates are suspension-feeders.
  - Seawater passes inside the animal via an incurrent siphon, through the pharyngeal gill slits, and into a ciliated chamber, the atrium.
  - Food filtered from the water is trapped by a mucous net that is passed by cilia into the intestine.
  - Filtered water and feces exit through an excurrent siphon.
  - The entire animal is encased in a tunic of a celluloselike carbohydrate.
- While the pharyngeal slits of the adult are the only link to the chordate characteristics, all four chordate trademarks are present in the larval forms of some tunicate groups.
- The larva swims until it attaches its head to a surface and undergoes metamorphosis, during which most of its chordate characteristics disappear.

Cephalochordates, also known as lancelets, closely resemble the idealized chordate.
- The notochord, dorsal nerve cord, numerous gill slits, and postanal tail all persist in the adult stage.
- Lancets are just a few centimeters long.
- They live with their posterior end buried in the sand and the anterior end exposed for feeding.
- Lancelets are suspension feeders, feeding by trapping tiny particles on mucus nets secreted across the pharyngeal slits.
  - Ciliary pumping creates a flow of water with suspended food particles into the mouth and out the gill slits.
  - In lancets, the pharynx and gill slits are feeding structures and play only a minor role in respiration, which primarily occurs across the external body surface.
- A lancet frequently leaves its burrow to swim to a new location.
  - Though feeble swimmers, their swimming mechanism resembles that of fishes through the coordinated contraction of serial muscle blocks.
  - Contraction of these chevron-shaped muscles flexes the notochord and produces lateral undulations that thrust the body forward.
  - The muscle segments develop from blocks of mesoderm, called somites, arranged serially along each side of the notochord of the embryo.

Molecular evidence suggests that the vertebrates’ closest relatives are the cephalochordates, and the urochordates are their next closest relatives.
- The evolution of vertebrates from invertebrates may have occurred in two stages.
  - In the first stage, an ancestral cephalochordate evolved from an organism that would resemble a modern urochordate larva.
  - In the second, a vertebrate evolved from a cephalochordate.
  - This first stage may have occurred through paedogenesis, the precocious development of sexual maturity in a larva.
  - Changes in the timing of expression of genes controlling maturation of gonads may have led to a swimming larva with mature gonads before the onset of metamorphosis.
  - If reproducing larvae were very successful, natural selection may have reinforced paedogenesis and eliminated metamorphosis.
  - The paedogenetic hypothesis is deduced from comparing modern forms, but no fossil evidence supports or contradicts this hypothesis.
  - Several recent fossil finds in China provide support for the second stage, from cephalochordate to vertebrate.
    - They appear to be “missing links” between groups.

Features that appear in these fossils include a more elaborate brain, eyes, a cranium, and hardened structures ("denticles") in the pharynx that may have functioned somewhat like teeth.

These fossils push the vertebrate origins to the Cambrian explosion.

Introduction to the Vertebrates

- Neural crest, pronounced cephalization, a vertebral column, and a closed circulatory system characterize the subphylum Vertebrata
  - The dorsal, hollow nerve cord develops when the edges of an ectodermal plate on the embryo's surface roll together to form the neural tube.
  - In vertebrates, a group of embryonic cells, called the neural crest, forms near the dorsal margins of the closing neural tube.
    - Neural crest contributes to the formation of certain skeletal elements, such as some of the bones and cartilages of the cranium, and other structures.
  - The vertebrate cranium and brain (the enlarged anterior end of the dorsal, hollow nerve cord) and the anterior sensory organs are evidence of a high degree of cephalization, the concentration of sensory and neural equipment in the head.
  - Organisms that have the neural crest and a cranium are part of the clade Craniata which includes the vertebrates and the hagfishes.
    - Hagfishes lack vertebrae but do have a cranium.
  - The cranium and vertebral column are parts of the vertebrate axial skeleton.
    - This provides the main support structure for the central trunk of the body and makes large body size and fast movements possible.
    - Also included in the axial skeleton are ribs, which anchor muscles and protect internal organs.
  - Most vertebrates also have an appendicular skeleton, supporting two pairs of appendages (fins, legs, or arms).
  - The vertebrate endoskeleton is made of bone, cartilage, or some combination of the two materials.
    - Although the skeleton is a nonliving extracellular matrix, living cells within the skeleton secrete and maintain the matrix.
    - The vertebrate endoskeleton can grow continuously, unlike the exoskeleton of arthropods.
  - Active movement by vertebrates is supported by ATP generated through aerobic respiration.
    - These movements may be to acquire prey or to escape predators.
  - Adaptations to the respiratory and circulatory systems support mitochondria in muscle cells and other active tissues.
    - These include a closed circulatory system, with a ventral, chambered heart that pumps blood through arteries and capillaries to provide nutrients and oxygen to every tissue in the body.
    - The blood is oxygenated as it passes through capillaries in gills or lungs.
  - An active lifestyle requires a large supply of organic fuel.
    - Vertebrate adaptations for feeding, digestion, and nutrient absorption help support active behavior.
    - These multiple adaptations in form and function to a variety of systems have supported the transition from a relatively sedentary lifestyle in pre-vertebrates to a more active one pursued by most vertebrates.
- An overview of vertebrate diversity
  - Our current understanding of vertebrate phylogeny is based on anatomical, molecular, and fossil evidence.
  - At the base are hagfishes and lampreys which lack hinged jaws.

All other vertebrates, the gnathostomes, have true jaws and also two sets of paired appendages.
In "fishes," including the cartilaginous fishes and three classes of bony fish, these paired appendages function in swimming.
In tetrapods, the appendages are modified as legs to support movements on land.
Among tetrapods, most amphibians lay eggs in water or an otherwise moist environment.
The other terrestrial tetrapods are amniotes, producing shelled, water-retaining eggs which allow these organisms to complete their life cycles entirely on land.
While most modern mammals do not lay eggs, they retain many of other key features of the amniotic mode of reproduction.
The traditional vertebrate group known as "reptiles" (turtles, snakes, lizards, crocodiles, and alligators) does not form a monophyletic group unless birds are included.

Jawless Vertebrates

- The two extant classes of jawless vertebrates, the agnathans, are the hagfishes and the lampreys.
These are eel-like in shape, but the true eels are bony fish.
The agnathans are an ancient vertebrate lineage that predates the origin of paired fins, teeth, and bones hardened by mineralization (ossification).
- Class Myxini: Hagfishes are the most primitive living "vertebrates"
All of the 30 or so species of hagfishes are marine scavengers, feeding on worms and sick or dead fish.
Rows of slime glands along a hagfish's body produce small amounts of slime to perhaps repulse other scavengers or larger amounts to deter a potential predator.
The skeleton of hagfish is made entirely of cartilage, a rubbery connective tissue.
In addition to a cartilaginous cranium, the hagfish notochord is also cartilaginous, providing support and a skeleton against which muscles can exert force during swimming.
Hagfishes lack vertebrae.
Therefore, they belong more precisely in the larger group of chordates, the Craniata, and are equated with the Vertebrata.
Hagfishes diverged from ancestors that produced the vertebrate lineage about 530 million years ago, during the early Cambrian.
- Class Cephalaspidomorphi: Lampreys provide clues to the evolution of the vertebral column
There are about 35 species of lampreys inhabiting both marine and freshwater environments.
The sea lamprey is an ectoparasite that uses a rasping tongue to penetrate the skin of its fish prey and to ingest the prey's blood and other tissues.
Sea lampreys live as suspension-feeding larvae in streams for years before migrating to the sea or lakes as predaceous/parasitic adults.
These larvae resemble the lancelets.
Some species of lampreys feed only as larvae.
After metamorphosis, they attain sexual maturity, reproduce, and die within a few days.
The notochord persists as the main axial skeleton in adult lampreys.
Lampreys also have a cartilaginous pipe surrounding the rodlike notochord.
Pairs of cartilaginous projections extend dorsally, partially enclosing the nerve cord with what might be a vestige of an early stage vertebral column.
In gnathostomes, the notochord is a larval structure, largely replaced during development by the segmental vertebrae.
Both hagfishes and lampreys lack skeleton-supported jaws and paired appendages.
A comparison of gnathostomes and agnathans shows that the brain and cranium evolved first in the vertebrate lineage.
This was followed by the vertebral column.

The jaws, ossified skeleton, and paired appendages evolved later.
This interpretation is consistent with the early Cambrian fossils in Chinese strata.

- Some extinct jawless vertebrates had ossified teeth and bony armor
  Jawless vertebrates are much more diverse and common in the fossil record than they are among today's fauna.
  A diversity of taxa informally called ostracoderms thrived from about 450 to 375 million years ago.
  Most species were less than 50 cm in length, lacked paired fins, and were apparently bottom dwellers.
  These probably wiggled along streambeds or the seafloor.
  Other species were more active with paired fins.
  Ostracoderm fossils show animals with circular or slitlike openings that lacked jaws.
  The majority of ostracoderms were probably deposit feeders (mud-suckers) or suspension feeders that trapped organic material on their pharyngeal apparatus.
  The pharyngeal apparatus of agnathans evolved into the major sites of gas exchange.
  Fossils of extinct agnathans provide evidence that mineralization of certain body structures evolved early in vertebrate history.
  An armor of bony plates encased ostracoderms.
  These may represent an early stage of ossification in which connective tissue is hardened when special cells secrete calcium and phosphate to form calcium phosphate, a hard mineral salt.
  Conodonts, which date back as far as 510 million years ago, had ossified cone-shaped toothlike structures in their mouths.
  Hagfishes have toothlike structures made of keratin, a structural protein.

Fishes and Amphibians

- During the late Silurian and early Devonian periods, gnathosomes largely replaced the agnathans.
- Chondrichthyes (the cartilaginous fishes) and Osteichthyes (bony fishes), and the extinct placoderms evolved during this time.
- In addition to jaws, fishes have two pairs of fins.
  Agnathans either lacked fins or had a single pair.
  Research in developmental genetics has shown that differential expression of some Hox genes may determine whether one or two sets of appendages develop in the embryos of extant vertebrates.
- Jaws and paired fins were major evolutionary breakthroughs.
  Jaws, with the help of teeth, enable the animal to grip food items firmly and slice them up.
  A jawed fish can exploit food supplies that were unavailable to earlier agnathans.
- Paired fins, along with the tail, enable fishes to maneuver accurately while swimming.
- With these adaptations, many fish species were active predators, allowing for the diversification of both lifestyles and nutrient sources.
- 1. Vertebrate jaws evolved from skeletal supports of the pharyngeal slits
  Vertebrate jaws evolved by modification of the skeletal rods that have previously supported the anterior pharyngeal slits.
  The remaining gill slits remained as the site of respiration.
  The Devonian period (about 360 to 400 million years ago) has been called the "age of fishes."
  Placoderms and another group of jawed fishes, the acanthodians, radiated in both fresh and salt water.
  Both dwindled and disappeared almost completely by the beginning of the Carboniferous period, about 360 million years ago.

A common ancestor to the placoderms and acanthodians may also have given rise to sharks and bony fishes some 425 to 450 million years ago.

- Class Chondrichthyes: Sharks and rays have cartilaginous skeletons

The class Chondrichthyes, sharks and their relatives, have relatively flexible endoskeletons of cartilage rather than bone.

In most species, parts of the skeleton are strengthened by mineralized granules, and the teeth are bony.

There are about 750 extant species, almost all in the subclass of sharks and rays, with a few dozen species in a second subclass the chimaeras, or ratfishes.

All have well-developed jaws and paired fins.

The cartilaginous skeleton of these fishes is a derived characteristic, not a primitive one.

The ancestors of Chondrichthyes had bony skeletons.

The cartilaginous skeleton evolved secondarily.

During the development of most vertebrates, the skeleton is first cartilaginous and then becomes ossified as hard calcium phosphate matrix replaces the rubbery matrix of cartilage.

The streamlined bodies of most sharks enable them to be swift, but not maneuverable, swimmers.

Powerful axial muscles power undulations of the body and caudal fin to drive the fish forward.

The dorsal fins provide stabilization.

While some buoyancy is provided by low density oils in large livers, the flow of water over the pectoral and pelvic fins also provides lift to keep the animal suspended in the water column.

Most sharks are carnivores that swallow their prey whole or use their powerful jaws and sharp teeth to tear flesh from animals too large to swallow.

In contrast, the largest sharks and rays are suspension feeders that consume plankton.

Shark teeth probably evolved from the jagged scales.

The intestine of shark is a spiral valve, a corkscrew-shaped ridge that increases surface area and prolongs the passage of food along the short digestive tract.

Acute senses are adaptations that go along with the active, carnivorous lifestyle of sharks.

Sharks have sharp vision but cannot distinguish colors.

Their acute olfactory sense (smelling) occurs in a pair of nostrils.

Sharks can detect electrical fields, including those generated by the muscle contractions of nearby prey, through patches of specialized skin pores.

The lateral line system, a row of microscopic organs sensitive to pressure changes, can detect low frequency vibrations.

In sharks, the whole body transmits sound to the hearing organs of the inner ear.

Shark eggs are fertilized internally.

Males transfer sperm via claspers on their pelvic fins to the reproductive tract of the female.

Oviparous sharks encase their eggs in protective cases and lay them outside the mother's body.

These hatch months later as juveniles.

Ovoviviparous sharks retain fertilized eggs in the oviduct.

The embryo completes development in the uterus, nourished by the egg yolk.

A few sharks are viviparous, providing nutrients through a placenta to the developing offspring.

Rays are closely related to sharks, but they have adopted a very different lifestyle.

Most rays are flattened bottom dwellers that crush mollusks and crustaceans in their jaws.

The enlarged pectoral fins of rays are used like wings to propel the animal through the water.

The tail of many rays is whiplike and may bear venomous barbs for defense against threats.

- Osteichthyes: The extant classes of bony fishes are the ray-finned fishes, the lobe-finned fishes, and the lungfishes

Bony fishes are the most numerous group of vertebrates, both in individuals and in species (about 30,000 species).

They range in size from 1 cm to more than 6 m.

They are abundant in the seas and in nearly every freshwater habitat.

Traditionally, all bony fishes were combined into a single class, Osteichthyes, but most systematists now recognize three extant classes: the ray-finned fishes, the lobe-finned fishes, and the lungfishes.

Nearly all bony fishes have an ossified endoskeleton with a hard matrix of calcium phosphate.

The skin is often covered with thin, flattened bony scales.

Like sharks, fishes can detect water disturbances through the lateral line system, part of which is visible as a row of tiny pits along either side of the body.

Bony fishes breathe by drawing water over four or five pairs of gills located in chambers covered by a protective flap, the operculum.

Water is drawn into the mouth, through the pharynx, and out between the gills by movements of the operculum and muscles surrounding the gill chambers.

The reproductive modes of fishes vary extensively.

Most species are oviparous, in which external fertilization occurs after the female sheds large numbers of small eggs and males synchronously release clouds of sperm (milt).

However, internal fertilization occurs in many fish groups and some are even viviparous.

Most fishes have an internal, air-filled sac, the swim bladder.

The positive buoyancy provided by air counters the negative buoyancy of the tissues, enabling many fishes be neutrally buoyant and remain suspended in the water.

The swim bladder evolved from balloonlike lungs that may have been used to breathe air when dissolved oxygen levels were low in stagnant shallow waters.

Bony fishes are generally maneuverable swimmers.

Their flexible fins are better for steering and propulsion than the stiffer fins of sharks.

The fastest bony fishes can swim up to 80 km/hr in short bursts.

The most familiar families of fishes belong to the ray-finned fishes, class Actinopterygii.

This class includes bass, trout, perch, tuna and herring.

In this group, the fins are supported by long flexible rays,

The fins may be modified for maneuvering, defense, and other functions.

Bony fishes, including the ray-finned fishes, probably evolved in freshwater and then spread to the seas during their long history.

Lobe-finned fishes (class Actinistia) have muscular pectoral and pelvic fins supported by extensions of the bony skeleton.

Many lobe-fins were large, bottom dwellers that may have used their paired, muscular fins to “walk” along the bottom.

Most Devonian coelacanths were probably freshwater animals with lungs, but others entered the seas during their evolution, including the only living genus, Latimeria.

Three genera of lungfishes (class Dipnoi) live today in the Southern Hemisphere.

They generally inhabit stagnant ponds and swamps.

They can gulp air into lungs connected to the pharynx of the digestive tract to provide oxygen for metabolism.

Lungfishes also have gills, which are the main organs for gas exchange in Australian lungfishes.
When ponds shrink during the dry season, some lungfishes can burrow into the mud and aestivate.
The ancestor of amphibians and all other tetrapods was probably a lungfish from the Devonian, a period when these fishes were dominant predators.

- Tetrapods evolved from specialized fishes that inhabited shallow water

Amphibians were the first tetrapods to spend a substantial portion of their time on land.
However, there were earlier vertebrate tetrapods that had relatively sturdy, skeleton-supported legs instead of paired fins, and which lived in shallow aquatic habitats.
During the Devonian period, a diversity of plants and arthropods already inhabited the land.
Trees and other large vegetation were transforming terrestrial ecosystems.
Plants at the edges of ponds and swamps and organic material deposited into aquatic habitats from terrestrial habitats also created new living conditions and food for fishes living near the water's edge.
A diversity of fishes resembling modern lobe-fins and lungfishes had already evolved.
These fishes (and modern frogs) used buccal pumping to breathe air.
In buccal breathing, the animal drops the floor of the mouth, drawing in air, and then closes the mouth and raises the floor, forcing the air into the lungs.
This supplemented gills for gas exchange.
At the water's edge, leglike appendages were probably better equipment than fins for paddling and crawling through the dense vegetation in shallow water.
The fossil record chronicles the transition to land over a 50-million-year period from 400 to 350 million years ago.
For example, fossils of Acanthostega not only have the bony support of gills but also the same basic skeletal elements as the walking legs of amphibians, reptiles, and mammals.
Acanthostega is representative of a period of vertebrate evolution when adaptations for shallow water preadapted certain fishes for a gradual transition to the terrestrial side of the water's edge.
As the earliest terrestrial tetrapods, amphibians benefited from abundant food and relatively little competition.
The Carboniferous, sometimes called "the age of amphibians," saw an adaptive radiation of amphibians.
Amphibians began to decline in numbers and diversity during the late Carboniferous.
As the Mesozoic era dawned about 245 million years ago, most surviving lineages of amphibians resembled modern species.

- Class Amphibia: Salamanders, frogs, and caecilians are the three extant amphibian orders

Today the amphibians (class Amphibia) are represented by about 4,800 species of salamanders (order Urodela, "tailed ones"), frogs (order Anura, tail-less ones"), and caecilians (order Apoda, "legless ones").
Some of the 500 species of urodeles are entirely aquatic, but others live on land as adults or throughout life.
On land, most salamanders walk with a side-to-side bending of the body that may resemble the swagger of the early terrestrial tetrapods.
The 4,200 species of anurans are more specialized than urodeles for moving on land.
Adult frogs use powerful legs to hop along the terrain.
Frogs nab insects by flicking out their sticky tongues.
Among adaptations that reduce predation, anurans may be camouflaged or secrete a distasteful, even poisonous, mucus from skin glands.

Many poisonous species are also brightly colored, perhaps to warn predators who associate the coloration with danger.

Apodans, the caecilians (about 150 species), are legless and nearly blind.

The reduction of legs evolved secondarily from a legged ancestor.

Superficially resembling earthworms, most species burrow in moist forest soil in the tropics.

A few South American species live in freshwater ponds and streams.

Amphibian means “two lives,” a reference to the metamorphosis of many frogs from an aquatic stage, the tadpole, to the terrestrial adult.

Tadpoles are usually aquatic herbivores with gills and a lateral line system, and they swim by undulating their tails.

During metamorphosis, the tadpole develops legs, the lateral line disappears, and gills are replaced by lungs.

Adult frogs are carnivorous hunters.

Many amphibians do not live a dualistic—aquatic and terrestrial—life.

There are some strictly aquatic, and some strictly terrestrial frogs, salamanders, and caecilians.

The larvae of salamanders and caecilians look like adults and are also carnivorous.

Paedomorphosis, the retention of some larval features in a sexually mature adult, is common among some groups of salamanders.

For example, the mudpuppy (Necturus) retains gills and other larval features when sexually mature.

Most amphibians retain close ties with water and are most abundant in damp habitats.

Those adapted to drier habitats spend much of their time in burrows or under moist leaves where the humidity is higher.

Most amphibians rely heavily on their moist skin to carry out gas exchange with the environment.

Some terrestrial species lack lungs entirely and breathe exclusively through their skin and oral cavity.

Amphibian eggs lack a shell and dehydrate quickly in dry air.

Most species have external fertilization, with eggs shed in ponds or swamps or at least in moist environments.

Some species lay vast numbers of eggs in temporary pools where mortality is high.

In contrast, others display various types of parental care and lay relatively few eggs.

In some species, males or females may house eggs on their back, in the mouth, or even in the stomach.

Some species are ovoviviparous or viviparous, retaining the developing eggs in the female reproductive tract until released as juveniles.

Many amphibians display complex and diverse social behavior, especially during the breeding season.

Then, many male frogs fill the air with their mating calls as they defend breeding territories or attract females.

In some terrestrial species, migrations to specific breeding sites may involve vocal communication, celestial navigation, or chemical signaling.

For the past 25 years, zoologists have been documenting a rapid and alarming decline in amphibian populations throughout the world.

Several causes that have been proposed include environmental degradation (especially acid rain) and the spread of a pathogen, a chytrid fungus.

Amniotes

- Evolution of the amniotic egg expanded the success of vertebrates on land

The amniote clade consists of the mammals, the birds, and the vertebrates commonly called reptiles, including turtles, lizards, snakes, and crocodiles.

The evolution of amniotes from an amphibian ancestor involved many adaptations for terrestrial living including:

- The amniotic egg.
- Waterproof skin.
- Increasing use of the rib cage to ventilate the lungs.

The amniotic eggs enabled terrestrial vertebrates to complete their life cycles entirely on land.

- In contrast to the shell-less eggs of amphibians, the amniotic eggs of most amniotes have a shell that retains water and can be laid in a dry place.
- The calcareous shells of bird eggs are inflexible, while the leathery eggs of many reptiles are flexible.
  - Most mammals have dispensed with the shell.
    - The embryo implants in the wall of the uterus and obtains its nutrition from the mother.
- Inside the shell of the amniotic egg are several extraembryonic membranes that function in gas exchange, waste storage, and the transfer of stored nutrients to the embryo.
  - These develop from tissues layers that grow out from the embryo.

• Vertebrate systematists are reevaluating the classification of amniotes

The amniotes are a monophyletic group (clade), with all modern reptiles, birds, and mammals sharing a common ancestor.

An evolutionary radiation of amniotes during the early Mesozoic era gave rise to three main groups, called synapsids, anapsids, and diapsids.

- These names are based on key differences in skull anatomy.
- The synapsids included mammal-like reptiles, the therapsids, from which mammals evolved.
- The anaspid lineage is probably extinct.
  - Turtles had been considered the only surviving anaspid lineage, but molecular comparisons place the turtles somewhere within the diapsids.
- The diapsids include most or all groups of modern reptiles (depending on the placement of turtles), as well as a diversity of extinct swimming, flying, and land-based reptiles.
- During the early Mesozoic radiation of amniotes, the diapsids split into two evolutionary branches, the lepidosaurs (including lizards, snakes, and tuataras) and the archosaurs (including crocodiles and alligators, dinosaurs, and birds).
  - The closest living relatives of birds are the crocodiles and alligators, but they are even more closely related to the extinct dinosaurs.
    - In fact, neither dinosaurs nor reptiles represent monophyletic taxa unless we also include birds.
- The classical classification of amniotes is at odds with several alternatives that are based on strict application of cladistic conventions, in which each taxa must represent a monophyletic group.
  - Some of the alternatives illustrate differences between “lumpers,” who prefer to minimize the number of taxa at each level and “splitters,” who prefer a finer-grained taxonomy with more taxa at each level.
  - Regardless of final classification, “reptile” is still a useful informal category for discussing all the amniotes except birds and mammals.
- In fact, all modern amniotes, including birds and mammals, evolved from forms that would probably be called “reptiles” if we saw them walking around today.

• A reptilian heritage is evident in all amniotes

Reptiles have several adaptations for terrestrial life not generally found in amphibians.
- Scales containing the protein keratin waterproof the skin, preventing dehydration in dry air.
- Reptiles obtain all their oxygen with lungs, not through their dry skin.
  - As an exception, many turtles can use the moist surfaces of their cloaca for gas exchange.
- Most reptiles lay shelled amniotic eggs on land.
- Fertilization occurs internally, before the shell is secreted as the egg passes through the female's reproductive tract.
- Some species of lizards and snakes are viviparous, their extraembryonic membranes forming a placenta that enables the embryo to obtain nutrients from its mother.
- Reptiles, sometimes labeled "cold-blooded," do not use their metabolism extensively to control body temperature.
  - However, many reptiles regulate their body temperature behaviorally by basking in the sun when cool and seeking shade when hot.
  - Because they absorb external heat rather than generating much of their own, reptiles are more appropriately called ectotherms.
    - One advantage of this strategy is that a reptile can survive on less than 10% of the calories required by a mammal of equivalent size.
- Reptiles were far more widespread, numerous, and diverse during the Mesozoic than they are today.
  - The oldest reptilian fossils date back to the Carboniferous period, about 300 million years ago.
  - Reptiles became the dominant terrestrial vertebrates for more than 200 million years in two great waves of adaptive radiation.
  - The first major radiation occurred during the early Permian and gave rise to the three main evolutionary branches: Synapsida, Anapsida, and Diapsida.
  - The second great radiation in the late Triassic was marked by the origin and diversification of the dinosaurs on land and the pterosaurs, or flying reptiles.
    - Pterosaurs had wings formed from a membrane of skin that stretched from the body wall, along the forelimb, to the tip of an elongated finger.
      - Stiff fibers provided support for the skin of the wing.
  - Dinosaurs were an extremely diverse group varying in body shape, size, and habitat.
    - There were two main dinosaur lineages: the ornithischians which were mostly herbivorous and; the saurischians which included both herbivorous and carnivorous dinosaurs.
      - The saurischians included the ancestors of birds.
    - There is increasing evidence that many dinosaurs were agile, fast-moving, and, in some species, social.
    - Paleontologists have discovered signs of parental care among dinosaurs.
    - There is continuing debate about whether dinosaurs were endothermic, capable of keeping their body warm through metabolism.
      - Some anatomical evidence supports this hypothesis, but many experts are skeptical.
      - In the warm, consistent Mesozoic climate, behavioral adaptations may have been sufficient for maintaining a suitable body temperature for terrestrial dinosaurs.
      - Also, large dinosaurs had low surface-to-volume ratios that reduced the effects of daily fluctuations in air temperature on the animal's internal temperature.
        - Regardless, the dinosaur that gave rise to birds was certainly endothermic,

as are all birds.
By the end of the Cretaceous, the dinosaurs became extinct.
Some paleontologists argue that a few species survived into the early Cenozoic.
It is uncertain whether the dinosaurs were undergoing a decline before they were finished off by an asteroid impact near the Yucatan Peninsula of Mexico.
There are about 6,500 species of extant reptiles, classified into four groups: Testudines (turtles); Sphenodontia (tuataras); Squamata (lizards and snakes); and Crocodilia (alligators and crocodiles).
In the traditional classification, these are orders within the class Reptilia.
In one alternative classification, each is a class.
Turtles evolved in the Mesozoic era and have scarcely changed since.
The usually hard shell is an adaptation that protects against predators.
Those turtles that returned to water during their evolution crawl ashore to lay their eggs.
Lizards are the most numerous and diverse reptiles alive today.
Most are relatively small.
Modern lizards nest in crevices and decrease their activity during cold periods, a strategy that may have enabled them to survive the Cretaceous "crunch."
Snakes are probably descendents of lizards that adapted to a burrowing lifestyle through the loss of limbs.
This limbless condition remains today, even though most snakes live above ground.
Vestigial pelvic and limb bones in primitive snakes such as boas, is evidence that snakes evolved from reptiles with legs.
Snakes are carnivorous and a number of adaptations aid them in hunting and eating prey.
Snakes have acute chemical sensors and are sensitive to ground vibrations.
The flicking tongue fans odors toward olfactory organs on the roof of the mouth.
Heat-detecting organs of pit vipers, including rattlesnakes, enable these night hunters to locate warm animals.
Some poisonous snakes inject their venom through a pair of sharp hollow or grooved teeth.
Loosely articulated jaws enable most snakes to swallow prey larger than the diameter of the snake itself.
Crocodiles and alligators (crocodilians) are among the largest living reptiles.
They spend most of their time in water, breathing air through upturned nostrils.
Crocodilians are confined to the tropics and subtropics.

- Birds began as feathered reptiles

Birds evolved during the great reptilian radiation of the Mesozoic era.
In addition to amniotic eggs and scales, modern birds have feathers and other distinctive flight equipment.
Almost every part of a typical bird's anatomy is modified in some way to enhance flight.
One adaptation to reduce weight is the absence of some organs.
For instance, females have only one ovary.
Modern birds are toothless and grind their food in a muscular gizzard near the stomach.
The skeletons of birds have several adaptations that make them light and flexible, but strong.
The bones are honeycombed to reduce weight without sacrificing much strength.
Flying requires a great expenditure of energy from an active metabolism.

- Birds are endothermic, using their own metabolic heat to maintain a constant body temperature.

Feathers and, in some species, a layer of fat provide insulation.

Efficient respiratory and circulatory systems with a four-chambered heart keep tissues well supplied with oxygen and nutrients.

- The lungs have tiny tubes leading to and from elastic air sacs that help dissipate heat and reduce body density.

Birds have excellent vision and excellent coordination, supported by well-developed areas of the brain.

- The large brains of birds (proportionately larger than those of reptiles or amphibians) support very complex behavior.

During the breeding season, birds engage in elaborate courtship rituals.

- This culminates in copulation, contact between the mates' vents, the openings to their cloacas.
- After eggs are laid, the avian embryo is kept warm through brooding by the mother, father, or both, depending on the species.

The most obvious adaptations for flight are wings.

- Wings are airfoils that illustrate the same principles of aerodynamics as airplane wings.
  - Pressure differences created by differences in air flow over the top and bottom of the convex wing lift the wing and the bird.
- Large pectoral (breast) muscles anchored to a keel on the sternum (breastbone) power flapping of the wings.
- Feathers are among the most remarkable of vertebrate adaptations.
  - They are both extremely light and strong.
  - Feathers are made of the protein keratin, the same material in reptile scales and mammalian hair and nails.
  - Feathers may have functioned first as insulation during the evolution of endothermy and were later co-opted as flight equipment.
  - Birds have downy feathers and contour feathers.
    - The downy feathers of birds lack hooks on barbules, producing a fluffiness that provides excellent insulation because of the trapped air.
  - Contour feathers are the stiff ones that contribute to the aerodynamic shapes of the wing and body.
    - The evolution of flight required radical alteration in body form but provides many benefits.
  - Flight enhances hunting and scavenging.
    - It enables many birds to exploit flying insects, an abundant, highly nutritious food resource.
    - Flight provides a ready escape from earthbound predators.
    - It enables many birds to migrate great distances to exploit different food resources and seasonal breeding areas.
      - The arctic tern migrates round-trip between the Arctic and Antarctic each year.

Cladistic analyses of fossilized skeletons support the hypothesis that the closest reptilian ancestors of birds were theropods.

- These were relatively small, bipedal, carnivorous dinosaurs (such as the velociraptors of Jurassic Park).
- While most researchers agree that the ancestor of birds was a feathered theropod, others place the origin of birds much earlier, from an ancestor common to both birds

and dinosaurs.
The most famous Mesozoic bird is Archeopteryx, known from fossils from Bavaria.
This ancient bird lived about 150 million years ago, during the late Jurassic period.
Archeopteryx had clawed forelimbs, teeth, and a long tail containing vertebrae.
Without its feathers, Archeopteryx would probably be classified as a theropod dinosaur.
Its skeletal anatomy indicates that it was a weak flyer, perhaps a tree-dwelling glider.
Archeopteryx is not considered to be the ancestor of modern birds, but probably an extinct side branch.
The evolutionary side branch that includes Archeopteryx probably stemmed from a common ancestor that also produced the lineage from which modern birds evolved.
In 1998, paleontologists described a diversity of Chinese fossils that may fill in the gap between dinosaurs and early birds such as Archeopteryx.
These include feathered but flightless dinosaurs which may have evolved feathers for thermoregulation or courtship displays.
Others have a much closer kinship to modern birds with a lack of teeth, a horny bill, and a short stubby tail.
There are about 8,600 extant species of birds classified in about 28 orders.
These include a few flightless birds, the ratites, which lack both a breastbone and large pectoral muscles.
The ratites include the ostrich, kiwi, and emu.
Most birds are carinates because they have a carina, or sternal keel, which anchor the large pectoral muscles.
Carinate birds exhibit a great variety of feather colors, beak and foot shapes, behaviors, and flying styles.
Nearly 60% of living bird species are in the order passeriformes, or perching birds.

- Mammals diversified extensively in the wake of the Cretaceous extinctions

With the extinction of the dinosaurs and the fragmentation of continents that occurred at the close of the Mesozoic era, mammals underwent an extensive adaptive radiation.
There are about 4,500 extant species of mammals.
Vertebrates of the class Mammalia were first defined by Linnaeus by the presence of mammary glands.
All mammalian mothers nourish their babies with milk, a balanced diet rich in fats, sugars, proteins, minerals, and vitamins, produced in the mammary glands.
All mammals also have hair, made of the keratin.
Hair and a layer of fat under the skin retain metabolic heat, contributing to endothermy in mammals.
Endothermy is supported by an active metabolism, made possible by efficient respiration and circulation.
Adaptations include a muscular diaphragm and a four-chambered heart.
Most mammals are born rather than hatched.
Fertilization is internal, and the embryo develops in the mother’s uterus.
In eutherian (placental) mammals and marsupials the lining of the uterus and extraembryonic membranes collectively form a placenta, where nutrients diffuse into the embryo’s blood.
The placenta in eutherians is more complex and provides a more intimate and longer-lasting association between the mother and her developing young.
Mammals generally have larger brains than other vertebrates of equivalent size.

- Many species are capable of learning.
- The relatively long period of parental care extends the time for offspring to learn important survival skills by observing their parents.

Feeding adaptations of the jaws and teeth are other important mammalian traits.

- Unlike the uniform conical teeth of most reptiles, the teeth of mammals come in a variety of shapes and sizes adapted for processing many kinds of foods.
- During the evolution of mammals from reptiles, two bones formerly in the jaw joint were incorporated into the mammalian ear and the jaw joint remodeled.

Mammals evolved over 220 million years ago from reptilian stock.

- The ancestor of mammals was among the therapsids.
- Extensive fossils show small stages in the evolution of the mammalian legs, skull, jaws, and teeth.
- While therapsids disappeared during the Mesozoic, mammals coexisted with dinosaurs and underwent a great adaptive radiation in the Cenozoic in the wake of the Cretaceous extinctions.
- Modern mammals are split into three groups: monotremes (egg-laying mammals), marsupials (mammals with pouches) and eutherian (placental) mammals.
  - Monotremes—the playtpuses and the echidnas—are the only living mammals that lay eggs.
    - The reptile-like egg contains enough yolk to nourish the developing embryo.
    - Monotremes have hair and females produce milk in specialized glands.
    - After hatching, the baby sucks milk from the mother's fur because they lack nipples.
  - Marsupials include opossums, kangaroos, bandicoots, and koalas.
    - A marsupial is born very early in development and in most species completes its embryonic development while nursing within a maternal pouch, the marsupium.
    - In most species, the tiny offspring climbs from the exit of the female's reproductive tract to the mother's pouch.
    - In Australia, marsupials have radiated and filled niches occupied by eutherian mammals in other parts of the world.
    - Through convergent evolution, these diverse marsupials resemble eutherian mammals that occupy similar ecological roles.
    - While marsupial mammals diversified throughout the Tertiary in South America and Australia, the placental mammals began an adaptive radiation on the northern continents.
      - Australia's isolation facilitated the diversification and survival of its marsupial fauna.
      - Invasions of placental mammals from North America impacted the marsupial fauna of South America about 12 million years ago and then again about 3 million years ago when the continents were connected by the Isthmus of Panama.
      - This mammalian biogeography is an example of the interplay between biological and geological evolution.
  - Compared to marsupials, eutherian mammals (placentals) have a longer period of pregnancy.
    - Young eutherians complete their embryonic development within the uterus, joined to the mother by the placenta.
    - Marsupials and eutherians are more closely related to each other than either is to monotremes.
      - Fossil evidence places the split between marsupials and eutherians at about 80 to 100 million years ago, but molecular evidence places it at least 125 million

years ago.

Adaptive radiation during the Cretaceous and early Tertiary periods produced the orders of eutherian mammals that we recognize today.

The current hypothesis for the evolutionary relationships among eutherian orders, based on molecular systematics, clusters them into four main clades.

The Afrotheria includes elephants, aardvarks, hyraxes, and manatees.

The order Edentata is composed of sloths, anteaters, and armadillos, all from South America.

The third clade includes the bats (Chiroptera), the "core insectivores" (such as shrews and moles), carnivores, artiodactyls (pigs, cows, camels, and hippos) and perissodactyls (horses and rhinoceroses), and cetaceans.

The discovery in late 2001 of an Eocene whale fossil with a foot skeleton very similar to that of hippos and pigs corroborates the molecular evidence.

The fourth (and largest) eutherian branch contains the lagomorphs (rabbits and relatives), rodents, and primates.

The order Rodentia ("gnawing"), with about 1,700 species, is the largest mammalian order and includes rats, mice, squirrels, and beavers.

The members of this order have incisors on both the upper and lower jaws that resist heavy wear by growing continuously.

Order Primates includes monkeys, apes, and humans.

Primates and the Evolution of Homo sapiens

- Primate evolution provides a context for understanding human origins

Primates are difficult to define unambiguously in terms of morphological attributes.

Most primates have hands and feet adapted for grasping.

Relative to other mammals, they have large brains and short jaws.

They have flat nails on their digits, rather than narrow claws.

Primates also have relatively well-developed parental care and relatively complex social behavior.

The earliest primates were probably tree dwellers, shaped by natural selection for arboreal life.

The grasping hands and feet of primates are adaptations for hanging on to tree branches.

All modern primates, except Homo, have a big toe that is widely separated from the other toes.

The thumb is relatively mobile and separate from the fingers in all primates, but a fully opposable thumb is found only in anthropoid primates .

The unique dexterity of humans, aided by distinctive bone structure at the thumb base, represents descent with modification from ancestral hands adapted for life in the trees.

Other primate features also originated as adaptations for tree dwelling.

The overlapping fields of vision of the two eyes enhance depth perception, an obvious advantage when brachiating.

Excellent hand-eye coordination is also important for arboreal maneuvering.

Primates are divided into two subgroups.

The Prosimii (prosimians), probably resemble early arboreal primates and include the lemurs of Madagascar and the lorises, pottos, and tarsiers of tropical Africa and southern Asia.

The Anthropoidea (anthropoids) include moneys, apes, and humans.

The oldest known anthropoid fossils, from about 45 million years ago, support the hypothesis that tarsiers are the prosimians most closed related to anthropoids.

By about 40 million years ago, monkeys were established in Africa, Asia, and South

America.
The Old World and New World monkeys underwent separate adaptive radiations.
All New World monkeys are arboreal, but Old World monkeys include arboreal and ground-dwelling species.
New World monkeys have prehensile tails and nostrils that open to the side, while Old World species lack prehensile tails and their nostrils open downward.
In addition to monkeys, the anthropoid suborder also includes four genera of apes: Hylobates (gibbons), Pongo (orangutans, Gorilla (gorillas), and Pan (chimpanzees and bonobos).
Modern apes are confined exclusively to the tropical regions of the Old World.
They evolved from Old World monkeys about 25-30 million years ago.
With the exception of gibbons, modern apes are larger than monkeys, with relatively long arms and short legs, and no tails,
Although all apes are capable of brachiating, only gibbons and orangutans are primarily arboreal.
Social organization varies among the genera, with gorillas and chimpanzees highly social.
Apes have relatively larger brains than monkeys, and their behavior is more flexible.

- Humanity is one very young twig on the vertebrate tree

In the continuity of life spanning over 3.5 billion years, humans and apes have shared ancestry for all but the last few million years.
Paleoanthropology is the study of human origins and evolution.
Paleoanthropology focuses on the tiny fraction of geologic time during which humans and chimpanzees diverged from a common ancestor.
Paleoanthropologists use two words that are easy to confuse but which have distinct meanings.
Hominoid is a term referring to great apes and humans collectively
Hominid has a narrow meaning, confined to those twigs of the evolutionary tree that are more closely related to us than to any other living species.
There are two main groups of hominids: the australopithecines, which came first and are all extinct, and members of the genus Homo, with all species extinct except one: Homo sapiens.
Paleoanthropology has a checkered history with many misconceptions about human evolution generated during the early part of the twentieth century that still persist in the minds of the general public, long after these myths have been debunked by fossil discoveries.
First, our ancestors were not chimpanzees or any other modern apes.
Chimpanzees and humans represent two divergent branches of the hominoid tree that evolved from a common ancestor that was neither a chimpanzee nor a human.
Second, human evolution did not occur as a ladder with a series of steps leading directly from an ancestral hominoid to Homo sapiens.
If human evolution is a parade, then many splinter groups traveled down dead ends and several different human species coexisted.
Human phylogeny is more like a multibranched bush with our species as the tip of the only surviving twig.
Third, the various human characteristics, such as upright posture and an enlarged brain, did not evolved in unison.
Different features evolved at different rates, called mosaic evolution.
Our pedigree includes ancestors who walked upright but had brains much less

developed than ours.

After dismissing some of the folklore on human evolution, we must admit that many questions about our own ancestry remain.

Human evolution is marked by the evolution of several major features.

Brain Size. Based on skull measurements, researchers have estimated that brain size in hominoids tripled over the past 6 million years.

It increased from about 400-450 cm3 in hominoids (and similar to modern chimpanzees) to about 1,300 cm3 in modern humans.

Jaw Shape. Our hominoid ancestors had longer jaws—prognathic jaws—than those of modern humans.

This resulted in a flatter face with more pronounced chins.

There were also changes in dentition.

Bipedal Posture. Based on fossil skeletons, it is clear that our hominoid ancestors walked on all four limbs when on the ground, like modern apes.

The evolution of bipedal posture—upright posture and two-legged walking—is associated with key skeletal modifications seen in early hominid fossils.

Reduced Size Differences Between the Sexes. In hominoids, a size difference between females and males is a major feature of sexual dimorphism.

On average, male gorillas and orangutans are twice as heavy as females and male chimps and bonobos are about 1.35 times heavier than females.

In humans, males average about 1.2 times the weight of females.

Some Key Changes in Family Structure. Fossils are effective at documenting evolutionary changes in morphological features, but not changes in social behavior.

Insights into social behavior are derived from comparisons between humans and other extant hominoids.

In contrast to most ape species, monogamy, with long-term pair-bonding between mates, prevails in most human cultures.

Newborn humans infants are exceptionally dependent on their mothers, and the duration of parental care (and opportunities for enhanced learning) is much longer in humans than in other hominoids.

All known hominid (human) fossils older than about 1.5 million years are from eastern and southern Africa.

Most consist of teeth and fragments of jaws, skulls, and other skeletal pieces, with a few spectacular exceptions.

Researchers must try to reconstruct human phylogeny from an incomplete record, revising their hypotheses to account for new fossil evidence and data from new research strategies such as molecular systematics.

The various pre-Homo hominids are classified in the genus Australopithecus ("southern ape") and are known as australopithecines.

The first australopithecine, A. africanus, was discovered in 1924 by Raymond Dart in a quarry in South Africa.

From this and other skeletons, it became clear that A. africanus probably walked fully erect and had humanlike hands and teeth.

However, the brain was only about one-third the size of a modern human's brain.

In 1974, a new fossil, about 40% complete, was discovered in the Afar region of Ethiopia.

This fossil, nicknamed "Lucy," was described as a new species, A. afarensis.

Based on this fossil and other discoveries, this species had a brain the size of a chimpanzee, a prognathic jaw, longer arms (for some level of arboreal locomotion), and sexual dimorphism more apelike than human.

However, the pelvis and skull bones and fossil tracks showed that A. afarensis walked bipedally.

In the past few years, paleoanthropologists have found hominid species that predate A. afarensis.

The oldest fossil that is unambiguously more human than ape is Australopithecus anamensis, which lived over 4 million years ago.

Other fossils of putative hominids go back 6 million years, closer to the ape-human split that molecular systematists estimate occurred about 5 - 7 million years ago.

One key question in paleoanthropology is which of the australopithicines were evolutionary dead ends and which were either on, or close to, the phylogenetic lineage that led to the Homo branch.

Two lineages appeared after A. afarensis: the “robust” australopithecines with sturdy skulls and powerful jaws and teeth for grinding and chewing hard, tough foods; and the “gracile” australopithecines with lighter feeding equipment adapted for softer foods.

Most researchers agree that the robust australopithecines were an evolutionary dead end, and that the ancestors of Homo were among the gracile australopithecines.

The earliest fossils that anthropologists place in our genus, Homo, are classified as Homo habilis.

These fossils range in age from 2.5 to 1.6 million years old.

This species had less prognathic jaws and larger brains (about 600 - 750 cm3) than australopithecines.

In some cases, anthropologists have found sharp stone tools with these fossils, indicating that some hominids had started to use their brains and hands to fashion tools.

A remarkably complete fossil of a young hominid known as “Turkana Boy” indicates that even larger brains had evolved by 1.6 million years ago.

The body had a brain that would probably be over 900 cm3 in an adult of his species, a size between that of H. habilis and H. erectus.

Homo erectus was the first hominid species to migrate out of Africa, colonizing Asia and Europe.

They lived from about 1.8 million to 500,000 years ago.

Fossils from Asia are known by such names as “Beijing man” and “Java Man.”

In Europe, H. erectus gave rise to the humans known as Neanderthals.

Compared to H. habilis, H. erectus was taller, had a larger brain (averaging about 1,100 cm3), and had about the same level of sexual dimorphism as modern humans.

The term Neanderthal is now used for humans who lived throughout Europe from about 200,000 to 40,000 years ago.

Fossilized skulls indicate that Neanderthals had brains as large as ours, though somewhat different in shape.

Neanderthals were generally more heavily built than modern humans.

Controversy surrounds the classification of fossils of the humans that lived in Europe, Asia, and Africa from about 500,000 to 100,000 years ago.

One school of researchers refers to all the regional forms as “archaic Homo sapiens," with subspecies names for the regional variants.

The other school restricts the name Homo sapiens to later fossils and gives separate species names to the regional fossils.

This difference reflects a debate between advocates of alternative hypotheses for the origin of modern humans.

- Two alternative hypotheses have been proposed for the origin of anatomically modern humans.
  - In the multiregional hypothesis, fully modern humans evolved in parallel from the many local populations of H. erectus.
    - In this view, the great genetic similarity of all modern people is the product of occasional interbreeding between neighboring populations.
  - The other hypothesis, the "Out of Africa" or replacement hypothesis, argues that all Homo sapiens throughout the world evolved from a second major migration out of Africa that occurred about 100,000 years ago.
    - This migration completely replaced all the regional populations of Homo derived from the first hominid migrations.
  - Both hypotheses recognize the fossil evidence for humanity's African origin.
    - The multiregional hypothesis places that last common ancestor in Africa over 1.5 million years ago, when H. erectus began migrating to other parts of the world.
    - According to the replacement hypothesis, all of the world's populations diverged from anatomically modern Homo sapiens that evolved from an African H. erectus population and then migrated throughout the world.
    - All of the regional descendents of H. erectus are therefore evolutionary dead ends.
    - A compromise alternative to these extremes suggests that Homo sapiens originated and then dispersed from Africa 100,000 years ago.
      - These individuals then interbred with the regional descendents of the earlier H. erectus migration.
      - This hypothesis predicts that the genomes of indigenous people from around the world today should reflect a complex mix of ancestries.
    - So far, the genetic data have mostly supported the replacement hypothesis.
      - Using changes in mitochondrial DNA (mtDNA) among human populations as a molecular clock, research has reported a time of genetic divergence of about 100,000 years ago.
        - This is supported by nuclear genetic markers.
      - The mtDNA extracted from Neanderthal bones fall completely outside the range of mtDNA for modern Europeans.
        - These data suggest that Neanderthals contributed nothing to the ancestry of anatomically modern humans in Europe.
      - To choose among these competing hypotheses, comparisons of Y chromosomes in 2001 provide perhaps the most important genetic data so far.

- The Y chromosome is passed from male to male through the generations of a family with a minimum of crossing over with the X chromosome.
  - The diversity among Y chromosomes is limited to mutations.
- By comparing the Y chromosomes of males from various geographic regions, researchers were able to infer divergence from a common African ancestor less than 100,000 years ago.

So far, the fossil evidence has been less one-sided than the genetic data in testing the alternative hypotheses.

- The western European fossil evidence is consistent with total replacement of Neanderthals about 40,000 years ago by anatomically modern humans, known as Cro-Magnons.
- There were no intermediates suggesting interbreeding between Neanderthals and the later arrivals.
  - However, fossil evidence from outside Europe is more ambiguous, with some paleoanthropologists interpreting some Asian fossils as intermediates between older fossils of H. erectus and the skeletal features of modern Asians.